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Abbreviations

AET	Actual Evapotranspiration
AI	Aridity Index
AIC	Akaike Information Criterion
AUC	Area Under The Curve
DEM	Digital Elevation Model
DistRoad	Distance To Closest Road
FN	Fundamental Niche
GIS	Geographic Information System
GLMM	Generalized Linear Mixed Model
GWR	Geographically Weighted Regression
IDW	Inverse Distance Weighted
MIREN	Mountain Invasion Research Network
OLS	Ordinary Least Squares
PAnnual	Annual Precipitation
PCold	Precipitation Of The Coldest Quarter
PDD	Positive Degree Days
PET	Potential Evapotranspiration
PWarm	Precipitation Of The Warmest Quarter
RN	Realized Niche
ROC	Receiver Operating Characteristic
SDM	Species Distribution Model
TAnnual	Annual Mean Temperature
TCold	Minimum Temperature Of The Coldest Month
TWarm	Maximum Temperature Of The Warmest Month

1 Abstract

Non-native species are a main cause for the global loss of biodiversity and ecosystem services. Mountain regions have been relatively spared from plant invasions up to now, mostly due to climatic restrictions and low human influence, with roads being the main pathways. But the invasion risk is increasing due to climate change and intensified land use. This is problematic, because mountain regions generally have high conservation value and are hard to manage. Therefore, prevention is crucial. The aim of my study is to improve predictions of plant invasions by including roads and topoclimate in the species distribution models and to provide suggestions for adequate roadside management.

First, I downscaled bioclimatic variables according to the topography to a resolution of 50 x 50 m, applying a geographically weighted regression. Then, I fitted a species distribution model on both the original and downscaled bioclimate ('topoclimate'), with a generalized linear mixed model. As response variable, I used presence-absence data for *Trifolium repens* (n=7683), which had been collected by the Mountain Invasion Research Network in 11 mountain regions worldwide. Furthermore, I fitted three species distribution models, based on 'topoclimate', 'topoclimate and roads' and 'roads'. I then evaluated all models with the area under the receiver operating characteristic curve, focusing especially on sensitivity values. For validation, I used an independent dataset from Victoria, Australia.

Both downscaling the bioclimate and including roads improved the species distribution models, with roads being an even more robust predictor than bioclimate. However, the overall predictive power of all models was very low, with moderate sensitivity values.

This limited predictive power on a regional level (in Victoria, Australia) can be partly explained by general issues regarding invasive species but also by local peculiarities of the validation area. More local information would be needed in order to make accurate predictions for regional management. However, the global importance of mountain roads as pathways for plant invasions was confirmed by my study, which emphasizes the need for adequate roadside management. Generally, management should focus on both preventive measures as well as controlling further spread, especially in high conservation value areas.

2 Popular scientific summary

Invasive species have gained public recognition worldwide due to the severe problems they can cause, e.g. outcompeting native species or triggering allergic reactions in humans. Ecologically, invasive species are seen as one of the main reasons for the global loss of biodiversity and ecosystem services. Financial losses due to invasive species are estimated to equal roughly 5 % of the world economy. In the future, such biological invasions and the problems associated with them are expected to increase even more.

In mountains however, the situation is not that bad. There are not many invasives yet due to the harsh climate and little human influence. Moreover, the prevention of future invasions is relatively easy, as introduction pathways are limited. Still, the problem should not be underestimated, because the invasion risk in mountains is constantly increasing (due to climate change and intensified land use) and invasive species are very hard to control once they have spread in these remote and rugged areas.

In my work, I focused only on plants (not on animals) and my main goal was to improve predictions of plant invasions in mountains. As study species, I chose White Clover (*Trifolium repens*), a widespread mountain invader. Usually, predictions of where a plant could potentially grow are only based on the climate (with a resolution of 1x1 km). In order to refine these predictions, I first downscaled the resolution of the climatic data to 50x50 m. Secondly, I included roads in the predictions as they are known to be the most important introduction pathway for plants in mountains. Both approaches improved the predictions indeed – however, I was not able to predict accurately the current species' distribution in Victoria, Australia. One of the main reasons for this was probably that I made predictions on a global scale, which of course can only give rough estimates. For accurate predictions on a local level, one would also have to take into account the particular local conditions, e.g. land use and current vegetation. Still, my results underlined the importance of roads for plant invasions in mountains – therefore it is crucial to monitor and manage roadsides adequately.

3 Introduction

Non-native species

Over the last decades, invasive species have gained public and academic recognition worldwide, mainly due to their severe economic and ecological **impacts** (Millennium Ecosystem Assessment *et al.* 2005; Lockwood *et al.* 2013). Global financial losses due to invasive species are estimated to equal roughly 5 % of the world economy; examples of such economic impacts being invasive pests in agriculture or infectious human diseases (Pimentel *et al.* 2001). Furthermore, invasive species are seen as one of the main reasons for the loss of global biodiversity and ecosystem services (Millennium Ecosystem Assessment *et al.* 2005). Ecological impacts range from genetic level (e.g. hybridization and introgression) over individuals (e.g. behavior adaptation to new predator), populations (e.g. changes in structure and abundance due to new competitor), communities (e.g. introduced herbivores altering the base of trophic web) to ecosystems (e.g. nitrogen-fixing plants changing soil properties) and finally the global level (e.g. global homogenization) (Lockwood *et al.* 2013).

Range expansion of species is a natural process and usually happens over long, geological time frames, whereas if it is **human-aided**, dispersal rates are orders of magnitude higher and geographic patterns change substantially (Lockwood *et al.* 2013; Petitpierre 2013). International sea, land and air connections for trade and travel establish new pathways for non-native species, helping them to overcome natural barriers and reach novel areas (Hulme 2009; Lockwood *et al.* 2013). Moreover, the rate of dispersal is much faster and it differs from natural dispersal in that individuals are usually released repeatedly and they stem from multiple source populations (Lockwood *et al.* 2013). Human-aided transport of species can happen either intentionally (e.g. as food, biofuel, game, biocontrol) or unintentionally (e.g. through ship ballast water, horticulture, roads) (Lockwood *et al.* 2013). Most of the human-transported species die during transportation or once they are released outside their native geographic range, but about 10 % of the species manage to survive, out of which 10 % are able to establish a population in their new environment (Williamson & Fitter 1996). Out of these established non-native species, again roughly 10 % become invasive (Williamson & Fitter 1996).

Species are considered **non-native** in areas outside their natural geographical range and dispersal potential (synonyms: alien, exotic, non-indigenous) (International Union for Conservation of Nature (IUCN) 2000; Richardson *et al.* 2000; Lockwood *et al.* 2013). There is a grey area of space and time between the differentiation of native and non-native species (Lockwood *et al.* 2013): on a spatial scale species can be non-native to continents, islands, bio- or ecoregions, states or counties and the temporal scale varies depending on the historical human activity in that area (e.g. European colonization of Australia) (Richardson *et al.* 2000).

Invasive species are non-native species that either spread massively (e.g. due to lack of predators and competitors) or have an economic or ecological impact (Richardson *et al.* 2000; Daehler 2001; Lockwood *et al.* 2013). Invasion should be seen as a process, not a classification of a species (Lockwood *et al.* 2013).

Even though only a small fraction of all transported species become invasive, their impact can be severe, as stated above. And in the **future**, biological invasions are expected to increase even more (Millennium Ecosystem Assessment *et al.* 2005; Bradley *et al.* 2010), with complex reactions to different aspects of global change. Rising temperature and altered precipitation patterns could both facilitate or hinder plant invasions, whereas rising carbon dioxide and nitrogen deposition generally favor invasive plants (Bradley *et al.* 2010). Intensified land use and increasing global commerce will accelerate invasions as the speed and scale of human movement continues to expand (Pysek *et al.*

2010; Lockwood *et al.* 2013). Overall, global change favors invasive over native species, because most invasive species have traits that are well-suited to change and they are often more successful with higher resource availability (Bradley *et al.* 2010). Biological invasions are therefore both cause and consequence of ecosystem changes (Lockwood *et al.* 2013; Petitpierre 2013). Furthermore, an 'invasion debt' is expected to add to future invasions – meaning that non-native populations often stay very small, sometimes undetected, for a long time before they suddenly spread (Ficetola *et al.* 2007; Lockwood *et al.* 2013).

Non-native plants in mountains

In mountain regions, there are relatively **few plant invasions up to now**, mainly due to climatic restrictions and low human influence (Pauchard *et al.* 2009; Alexander *et al.* 2011; Kueffer 2011; McDougall *et al.* 2011; Pyšek *et al.* 2011; Marini *et al.* 2012; Otto *et al.* 2014; Byun *et al.* 2015; González-Moreno *et al.* 2015; Lembrechts *et al.* 2016). The process called 'directional ecological filtering' describes the progressive dropping out of non-native species with elevation, whereby the species reaching highest elevations are the ones having the broadest climatic tolerances – and not specialized stress-tolerant species, like it is the case for native species (Alexander *et al.* 2011). This suggests that non-native plants first arrive at low elevations, where anthropogenic propagule pressure is highest, and spread upwards from there – meaning that invasion resistance in mountains is not mainly determined by extreme climatic conditions, but instead by the pathways of introduction (Alexander *et al.* 2011).

Despite the currently low invasion success in mountains, the **invasion risk is increasing** due to climate change and intensified land use (Pauchard *et al.* 2009, 2016; Kueffer 2011; McDougall *et al.* 2011; Petitpierre 2013). With climate change, alpine areas are expected to experience above average warming (Walther *et al.* 2005). And with increasing temperatures, both native and non-native species distribution ranges can expand to higher latitudes and elevations (Lenoir *et al.* 2008; Pauchard *et al.* 2016). In addition to climate change, intensified land use with increasing tourism accelerates the invasion process as it enhances disturbance, connectivity and propagule pressure (Kueffer 2011; Pyšek *et al.* 2011; Pauchard *et al.* 2016). This is even more concerning considering the aspect that mountain plant communities have a lower invasion resistance than lowland communities (Lembrechts *et al.* 2014).

Propagule pressure is defined by the number of released individuals (i.e. propagule size), their characteristics like health, age and phenotypes (i.e. propagule composition) and the amount of release events (i.e. propagule number) (Lockwood et al. 2013).

Plant invasions in mountains are especially **problematic** because these regions generally have a high conservation value and they provide important ecosystem services like fresh water supply (Pauchard *et al.* 2009). Since mountains are relatively isolated ecosystems, they are also rich in endemic species and centers of significant biodiversity (International Union for Conservation of Nature (IUCN) 2000; Alexander *et al.* 2011). This evolutionary isolation means that native species are especially vulnerable to the introduction of novel species (International Union for Conservation of Nature (IUCN) 2000). Furthermore, plant invasions in mountainous areas are extremely hard to manage due to the rugged terrain and inaccessibility (McDougall *et al.* 2011).

Over the last decades, a general **upward trend of species ranges** has already been documented (Walther *et al.* 2005; Lenoir *et al.* 2008, 2010; Pauchard *et al.* 2009, 2016; Pyšek *et al.* 2011; Lembrechts *et al.* 2016). Numbers about the current situation of plant invasions in mountains vary slightly. According to (Pauchard *et al.* 2009), over 1000 non-native plant species have become established worldwide in high elevations above the treeline. Kueffer (2011) mentions 1500 non-native plant species in mountain areas worldwide and highlights woody plants as especially problematic (because they change the vegetation structure, fire regimes and chemical properties of the soil), as well as introduced garden plants that are pre-adapted to mountain climate (these specialists pose a greater threat than the currently common generalists). Invasions of such horticultural mountain specialists are expected to rise due to an increase in (transcontinental) tourism, recreation and residential habitation (Pauchard *et al.* 2009; Kueffer *et al.* 2014). Furthermore, nitrogen fixing plants have great invasive potential in cold climates (Hiltbrunner *et al.* 2014).

Because of this high risk, **prevention of plant invasions** is crucial in mountain areas (McDougall *et al.* 2011). The implementation of prevention measures is fortunately also relatively feasible in mountains due to the limited number of pathways, which makes prevention a realistic strategy (Pauchard *et al.* 2009, 2016; McDougall *et al.* 2011).

Non-native plants along mountain roads

Roads are seen as the main pathway for non-native plants entering alpine areas (Alexander *et al.* 2009; McDougall *et al.* 2011; Lembrechts *et al.* 2016). It is generally known that **vehicles** significantly increase the dispersal of plants and they are a major vector for the ongoing spread of non-native plants (Gelbard & Belnap 2003; Ansong & Pickering 2013; Lockwood *et al.* 2013; Otto *et al.* 2014). Especially long-distance dispersal is enhanced by vehicles, as seeds can stay attached to them for hundreds of kilometers (Von Der Lippe & Kowarik 2007; Taylor *et al.* 2012).

Mountain **roadsides** facilitate invasions because of enhanced propagule pressure and improved abiotic conditions like altered microclimate, hydrology, soil ecology and nutrient content (especially important in nutrient poor mountain ecosystems), moreover they are disturbed areas with less competition (Forman & Alexander 1998; Müllerová *et al.* 2011; Lembrechts *et al.* 2016).

Non-native plant species are observed to have **higher elevational ranges along roadsides**, which means that roadsides can serve as corridors for plant migration (Lembrechts *et al.* 2016). And because mountain roads pass through steep climatic and environmental gradients over a short distance (Pauchard *et al.* 2009; McDougall *et al.* 2011), they play an outstanding role in helping non-native plants to cross natural barriers and accelerate climate change induced range shifts (Lembrechts *et al.* 2016). In contrast to this vertical movement along roadsides, horizontal **spreading away from the roadsides** into the natural vegetation has been limited so far (Leung *et al.* 2009; Pollnac *et al.* 2012; Seipel *et al.* 2012; Lembrechts *et al.* 2014; Otto *et al.* 2014; Pollnac & Rew 2014). Therefore, roadsides can serve as an important early detection system where range shifts become visible first (Lembrechts *et al.* 2016). In order to react in time and prevent mountain invasions, it is helpful to refine predictions of future invasions (Thuiller *et al.* 2005b; Jiménez-Valverde *et al.* 2011; Petitpierre 2013), e.g. by including roads in the computations (González-Moreno *et al.* 2015; Lembrechts *et al.* 2016).

Current research and aim of my work

Biological invasions are usually predicted using species distribution models (SDMs), which aim at identifying places that are suitable for the survival of populations (Rödder *et al.* 2009; Soberón & Nakamura 2009). SDMs can be created by relating known species distribution data (presence, presence-absence or abundance data) with information about the environmental conditions at these locations (Guisan & Thuiller 2005; Elith & Leathwick 2009; Jiménez-Valverde *et al.* 2011). Based on this information, the species ecological niche can be characterized and then projected into geographic space, resulting in a map showing the species potential distribution (Rödder *et al.* 2009). There are different types of SDMs, depending e.g. on data availability, purpose and scale of the study. The most common strategy is to work with a set of up to 19 classical **bioclimatic variables at 30´´ resolution** (ca. 1x1 km at the equator) or a coarser resolution (Hijmans *et al.* 2005; Warren *et al.* 2008; Sears *et al.* 2011; Slavich *et al.* 2014; González-Moreno *et al.* 2015) and widely available **presence-only data** as response variable (Soberón & Peterson, A. Townsend 2005; Elith & Leathwick 2009; González-Moreno *et al.* 2015).

In my case, I will **downscale** all explanatory variables to a resolution of 50x50 m and test if this finer resolution allows a better prediction of the species distribution. First, for plants as **sessile** organisms a finer resolution usually yields more accurate predictions (Guisan & Thuiller 2005). Second, factors influencing the distribution of species are **scale** dependent: while on a global scale macroclimate is a main driver (i.e. original bioclimatic variables), on a regional level topography and fine-scale variations in climate gain importance (i.e. downscaled bioclimatic variables) (Elith & Leathwick 2009; Illán *et al.* 2010; Slavich *et al.* 2014). Third, the **terrain** matters: while macroclimatic data might be sufficient in flat terrain, in mountainous areas microclimate varies noticeably over short distances due to the rugged terrain (Gottfried *et al.* 1999; Guisan & Thuiller 2005; Holden *et al.* 2011; Sears *et al.* 2011; Opedal *et al.* 2015). Thus, there is need for fine-scale models to adequately predict species distributions in mountain regions (Illán *et al.* 2010; Scherrer & Körner 2011; Graae *et al.* 2012; Opedal *et al.* 2015) and it has been found that topoclimatic variables can significantly improve on macroclimatic variables for modeling species distributions (Slavich *et al.* 2014; Meineri & Hylander 2016). Also plant migration paths in mountains are found to be mainly determined by relief and surface texture (Gottfried *et al.* 1999; Opedal *et al.* 2015). Therefore it might be helpful in my case to downscale the explanatory variables. I will furthermore test if **including roads** as a factor improves the SDM. Since both large- and local-scale factors affect invasions, they should both be integrated in the SDMs to improve predictions (Ficetola *et al.* 2007). More precisely, it is recommended to use environmental data in tandem with corridors of propagule pressure when modelling invasive species distribution (Peterson 2003; Thuiller *et al.* 2005b; Jiménez-Valverde *et al.* 2011). And as explained above, it is generally known that roads have a strong influence on the distribution of non-native species in mountains. The dataset I will use includes **presence- and absence-data**.

With this approach, I am aiming to refine the distribution predictions for invasive plants in mountains. In particular, I want to answer the questions: Does downscaling the climatic variables improve the SDM in my case? How does including the factor 'distance to road' change the SDM? And how can roadside management counteract plant invasions? I will conduct my study with the example of *Trifolium repens* L. (White Clover), family Fabaceae, in 11 selected mountain regions worldwide (see chapter 4.1.1).

4 Material and Methods

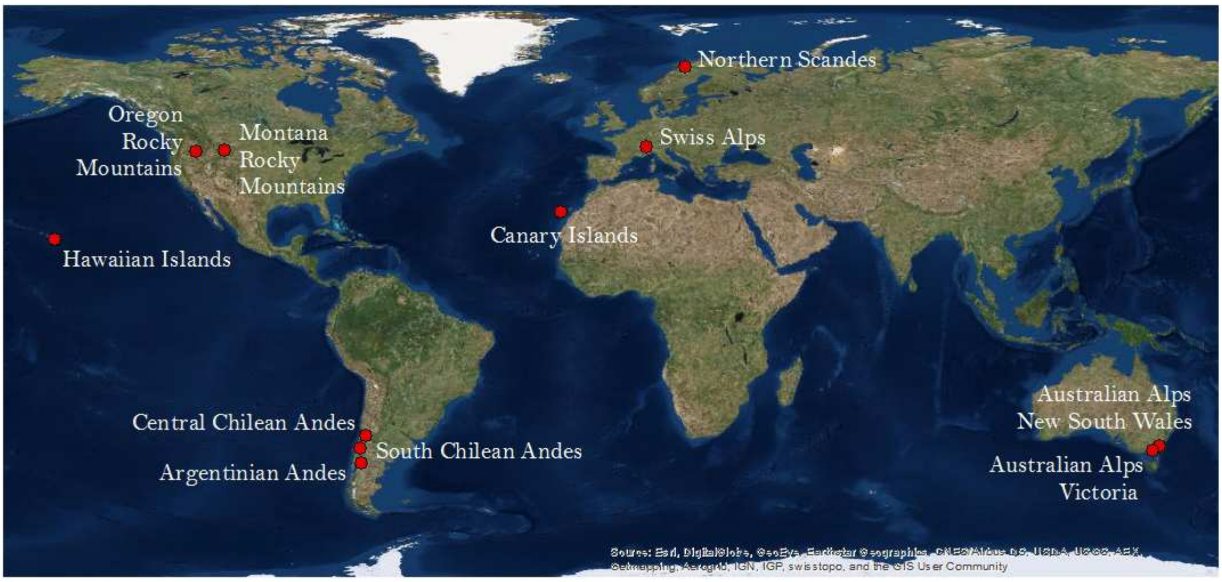
4.1 Data collection

4.1.1 Presence-absence-data for *Trifolium repens* (White Clover)

MIREN dataset

The plant data for my study was collected by the **MIREN** network (Mountain Invasion Research Network), www.mountaininvasions.org. MIREN is a worldwide collaboration of scientists in mountain regions that cover all major climatic zones and include island as well as continental systems (Kueffer *et al.* 2014). The aim of MIREN is to understand the effects of global change on plant invasions and plant biodiversity in mountainous areas, through standardized observational and experimental studies (Kueffer *et al.* 2014).

The dataset I used is the result of an **observational study** which aimed at investigating global patterns of plant invasions into mountains in relation to elevation and distance to roads (McDougall *et al.* 2011; Kueffer *et al.* 2014). This study has been conducted in 11 MIREN regions, shown in Figure 1. In each region, 3 mountain roads were chosen that extended over broad elevation gradients (between 618-1715 elevational meters), in order to capture most of the environmental variation within each region. All roads were open to traffic, at least during parts of the year. The survey was first conducted in summer 2007 and repeated in summer 2012. A list of all 11 regions, and if required regional adaptations to the general procedure, can be found in Appendix I: Characteristics of the 11 MIREN regions.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 1: Map of the 11 MIREN regions.

Along each road, 20 transects were evenly stratified by elevation, whereby the side of the road was chosen at random. Each transect was "T"-shaped and consisted of 3 plots, with Plot 1 being parallel to the road and Plot 2 and 3 perpendicular to it, stretching away from the center of Plot 1 (see Figure 2). Each plot measured 2 x 50 m, meaning that each transect reached 102 m away from the road. In the first survey in 2007, the plots were subdivided into smaller subplots of 2 x 10 m. Within the plots and subplots, the presence and absence of all vascular plants, both native and non-native, were recorded. Minor deviations from this survey design occurred in some regions due to local practicalities. In total, the dataset currently contains 7683 data points.

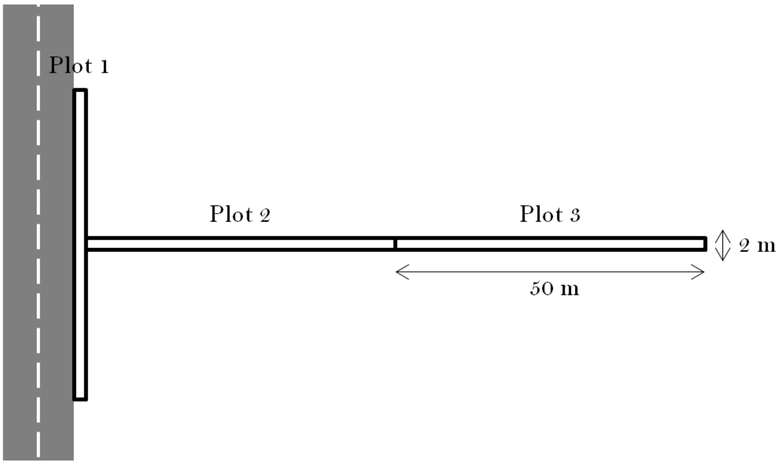


Figure 2: Schematic transect along mountain road.

Trifolium repens **(White Clover)**

In my study, I focused on *Trifolium repens*, which occurs in 10 of the 11 MIREN regions (all but the Canary Islands), in almost 10 % of all plots, with 757 presence points in total. It can be considered **native in the Swiss Alps and non-native in all other regions**, including the Northern Scandes (Lembrechts *et al.* 2014). *T. repens* is native to Europe and East Asia, but has also naturalized on the American continent, Australia and New Zealand and is one of the most widely distributed legumes in the world (Global Invasive Species Database (GISD) 2015).

T. repens thrives best in **temperate climates** (Global Invasive Species Database (GISD) 2015) with an optimum growing temperature between 20-25 °C and an optimal annual rainfall of above 750 mm (Australian Government (Department of Health and Ageing) 2008; Food and Agriculture Organization of the United Nations (FAO) 2016). Summer droughts are limiting growth in warm climates (Lane *et al.* 2000), whereas in cold climates growth is restricted by cold-induced water stress (if root temperature is below 5 °C) (Food and Agriculture Organization of the United Nations (FAO) 2016). In New Zealand, *T. repens* was found to be frost tolerant until -8 °C (Caradus 1995). Generally, a high degree of genetic variability and phenotypic plasticity allow *T. repens* to survive in highly variable environments (Lane *et al.* 2000).

T. repens is a perennial forb that propagates sexually by seeds as well as vegetatively by stolons (Food and Agriculture Organization of the United Nations (FAO) 2016). It can also behave as an annual in warm climates or under moisture stress (Australian Government (Department of Health and Ageing) 2008). Ansong & Pickering (2013) analyzed 13 studies about non-native seed **dispersal** by cars and found *T. repens* to be one of the most common species transported by cars. Since *T. repens* exhibits low shade tolerance, it benefits from disturbance (Ansong & Pickering 2013), which makes it predestinated for invading roadsides. Moreover, it is often intentionally introduced to help reduce soil erosion due to its capability to colonize bare, shallow soil (Global Invasive Species Database (GISD) 2015). Its stoloniferous growth and phenotypic plasticity make it also highly suitable for grazing and mowing, thus it is widespread on pastures and meadows (Olsen *et al.* 2008; Food and Agriculture Organization of the United Nations (FAO) 2016). It is often sowed in pastures and can be dispersed by cattle, sheep and goats as seeds can remain viable for several days after being ingested (Australian Government (Department of Health and Ageing) 2008). In general, species of European pastures, like *T. repens*, are considered to be the most widespread plant invaders in mountains and they were often already introduced during an early phase of livestock grazing (Kueffer 2011).

T. repens can have an **impact** on invaded ecosystems by symbiotically fixing atmospheric nitrogen and thus increasing soil fertility (Nesheim & Boller 1991; Hiltbrunner *et al.* 2014; Food and Agriculture Organization of the United Nations (FAO) 2016). However, in mountains, the contribution of nitrogen derived from symbiotic sources is generally small compared to nitrogen derived from mineralization (Körner 2003). For *T. repens* in particular, Nesheim & Boller (1991) showed that the amount of fixed nitrogen per plant decreases with temperature and also the capacity to compete with other plants in cold climates is limited by its slower growth and nitrogen accumulation. Conversely, Hiltbrunner *et al.* (2014) found that the genera *Trifolium* shows high nitrogen fixation activities at high elevations and that alpine life conditions generally seem favorable for symbiotic nitrogen fixation. Also Thomas & Bowman (1998) stated that alpine *Trifolium* species can influence the abundance and growth of plant species growing near them, both in a facilitative or inhibitive way. Surely, any increase in soil nitrogen can alter plant communities, generally reducing biodiversity and facilitating invasions (Bradley *et al.* 2010; Lockwood *et al.* 2013). Cold biomes in particular show a high potential to be transformed by nitrogen fixing plants and they have only little capacity to retain nitrogen, which leads to increased nitrate leaching and nitrous oxide emissions (Hiltbrunner *et al.* 2014). Therefore, analogous to atmospheric nitrogen deposition, nitrogen fixing plant invasions should be seen as significant threat, especially in cold biomes (Hiltbrunner *et al.* 2014). Another potential impact of *T. repens* is its ability to serve as a host for pests like the aphids *Myzus cymbalariae*, *Aulacorthum solani* and *Rhopalosiphum padi* that can affect endemic species, as it has been found on the Amsterdam Islands (Hullé *et al.* 2010). The impact of non-native *T. repens* in natural areas is generally considered moderate to high (Pickering & Hill 2007). Managing established populations of non-native *T. repens* requires a high level of effort – e.g. in Australia it is considered feasible to control vegetative regeneration, but not the seed bank (Pickering & Hill 2007).

Independent Australian dataset for validation

Independent presence-absence-data of *T. repens* was available on the 'Atlas' website, which is an Australian governmental database of flora and fauna records in New South Wales (New South Wales government 2016). The data can be downloaded as a point shapefile and it stems from various sources, including e.g. floristic surveys, Botanical Garden databases or reports from National Parks, that all follow the same survey guidelines. It is not a complete inventory of all species or locations, but it contains detailed distribution data for *T. repens* within the validation area (30721 km^2) with 626 presence and 5330 absence points. These data points were collected between 1972 and 2014 with varying spatial accuracy – data collected before the widespread use of a Global Positioning System (GPS) is limited to 100 m accuracy.

4.1.2 Explanatory variables for species distribution models (SDMs)

I selected the explanatory variables for the SDMs based on (1) comparable studies about species distribution modeling, (2) the physiology of *T. repens* and (3) data availability. Generally, it is recommended to focus on causality, i.e. the ecological basis, when selecting explanatory variables for SDMs (Araújo & Guisan 2006) and using not too complex relationships minimizes overfitting (Jiménez-Valverde *et al.* 2011).

WorldClim provides global **bioclimatic** data in a spatial resolution of 30´´ (ca. 1x1 km at the equator), based on the interpolation of temperature and precipitation recorded between 1950-2000 by globally distributed weather stations (Hijmans *et al.* 2005). Bioclimatic variables like 'Maximum temperature of the warmest month' are suitable for global SDMs, as they are independent of latitude and therefore worldwide comparable (Rödder & Lötters 2009). For the same reason, I did not take elevation into account: elevation reflects general altitude phenomena (e.g. atmospheric pressure, UV-B radiation) as well as regional characteristics (e.g. precipitation, wind velocity) so the same elevation can have different physiological 'meanings' in different regions (Guisan & Zimmermann 2000; Körner 2007; Rödder *et al.* 2009; Jiménez-Valverde *et al.* 2011). Concerning the bioclimatic variables, I chose a mixture of trends (annual values) and extremes (minimum/maximum values) that were found to be non-collinear and have been used in comparable studies, see Appendix II: Explanatory variables used in other studies (Guisan & Theurillat 2000; Thuiller *et al.* 2005a, b; Ficetola *et al.* 2007; Broennimann *et al.* 2012; Capinha *et al.* 2012; Petitpierre 2013; Tingley *et al.* 2014; González-Moreno *et al.* 2015). Out of these variables, I selected the ones that were likely to influence the physiology of *T. repens* the most (see chapter 4.1.1 and Table 1): Annual mean temperature (TAnnual), Maximum temperature of the warmest month (TWarm), Minimum temperature of the coldest month (TCold), Annual precipitation (PAnnual), Precipitation of the warmest quarter (PWarm) and Precipitation of the coldest quarter (PCold). Furthermore, I included the variables Aridity Index (AI) and Positive Degree Days (PDD). The Aridity Index is derived by dividing mean annual precipitation by mean annual potential evapotranspiration, so it indicates actual moisture availability for the potential growth of vegetation (Consortium for Spatial Information (CGIAR-CSI) 2016). PDD are the sum of positive degree days throughout one year and were computed by multiplying each monthly mean temperature (negative values were replaced with 0 °C) with the number of days per month and in the end adding up all monthly values. PDD indicate actual temperature conditions for vegetation on the ground, since there are no freezing temperatures under snow cover, and they approximate the length of the growing season. Since all above mentioned variables were either directly provided by WorldClim or calculated based on this data, all files have the same resolution of 30´´.

Table 1: Explanatory variables for modeling the distribution of *Trifolium repens*

Variable	Abbreviation	Relevance for *Trifolium repens* *
Annual mean temperature	TAnnual	thrives best in temperate climate
Maximum temperature of the warmest month	TWarm	optimal growing temperature between 20-25 °C; summer droughts are limiting growth
Minimum temperature of the coldest month	TCold	frost tolerant until -8 °C
Annual precipitation	PAnnual	annual rainfall > 750 mm promotes growth
Precipitation of the warmest quarter	PWarm	summer droughts limit growth
Precipitation of the coldest quarter	PCold	snow cover attenuates cold temperatures on the ground (frost tolerance)
Aridity Index	AI	indicates actual moisture availability (including potential evapotranspiration) for potential growth
Positive degree days	PDD	indicates length of growing season as well as actual temperature conditions on the ground (under snow)
Distance to closest road	DistRoad	better growing conditions and higher propagule pressure closer to roads

* Full explanation and sources can be found in chapter 4.1.1.

In addition to bioclimatic variables, I included '**distance to closest road'** (DistRoad) as a factor in a separate SDM to see which effect roads have on the distribution of *T. repens.* Based on the open access 'gROADS' data, which is available in the form of linear shapefiles (Socioeconomic Data and Applications Center (SEDAC) 2016), I created a raster file for the MIREN region 'Australian Alps Victoria' in ArcGIS 10.1 (ESRI), using the Euclidean distance tool. The resulting raster file had a spatial resolution of 50x50 m with cell values representing the distance to the closest road.

4.1.3 Topographic variables for downscaling bioclimatic data

I downscaled the bioclimatic raster files with the use of topographic variables (Guisan & Theurillat 2000; Ninyerola *et al.* 2000; Guisan & Thuiller 2005; Slavich *et al.* 2014; Meineri & Hylander 2016). All topographic variables are based on the satellite-based Digital Elevation Model (DEM), which has a spatial resolution of 1´´ (ca. 50x50 m at the equator) and an accuracy of 20 m vertically and 30 m horizontally (U.S. Geological Survey (USGS) 2016). Based on the DEM (which gives direct information about '**Elevation'**), I derived in ArcGIS the variables '**Slope**', '**Aspect**' and '**Solar Radiation**' using the correspondingly named tools. Aspect values are originally measured clockwise and range between 0° and 360° (lowest and highest value both mean northward) and flat areas are given the value -1. Thus, aspect values cannot be used directly for linear regression analysis and I separated them into '**Northness**' (i.e. cos(aspect) with values close to +1 if the aspect is northward and close to -1 if the aspect is southward) and '**Eastness**' (i.e. sin(aspect) with values close to +1 if the aspect is eastward, close to -1 if the aspect is westward). Solar Radiation was not calculated for the entire year, but only for the longest day of the year as an approximation for annual solar radiation, due to the computing intensity of these calculations. The cell values in the output raster represent the average incoming watt hours per square meter. In addition to the topographic variables, I calculated the '**Distance to ocean**' using the Euclidean distance tool in GIS, based on globally available shoreline information (National Centers for Environmental Information - National Oceanic and Atmospheric Administration (NOAA) 2016), which resulted in a raster file with a spatial resolution of 50x50 m.

4.2 Data analysis

4.2.1 Outline

I downscaled the bioclimatic data based on topographic variables on a regional level, for 5 MIREN regions in total. Based on this downscaled bioclimatic data, I fitted a species distribution model ('SDM downscaled') for *T. repens.* In addition, I fitted an analogous 'SDM original' based on the original bioclimatic data. I then compared these two SDMs, using an independent dataset from Australia as well as the training data, in order to assess the effect of downscaling the bioclimatic variables. Figure 3 shows the workflow diagram of this procedure and a more detailed description of the analysis can be found in chapter 4.2.2.

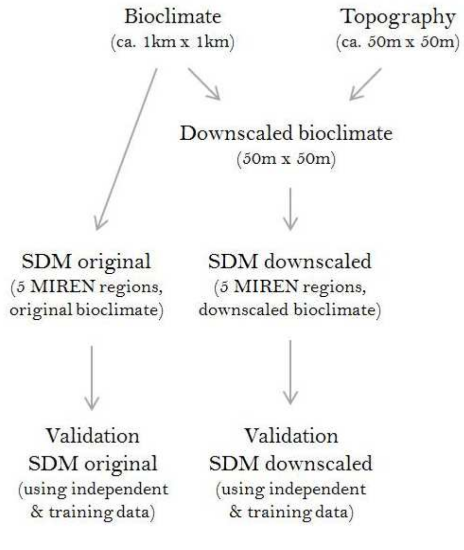


Figure 3: Workflow diagram of downscaling bioclimatic data.

I then added the bioclimatic data from the 6 MIREN regions that have not been downscaled due to time limitations (5 downscaled plus 6 not downscaled) and created a global model, based on only bioclimatic variables ('SDM I'). In a separate model, I added distance to the closest road as an extra factor ('SDM II'). And finally, I fitted a model only based on distance to the closest road ('SDM III'). Again, I compared the model performance and predictive power of the three SDMs, using independent data from Australia and the training data, to see the effect of including roads in the SDMs. A workflow diagram of this analysis can be seen in Figure 4 and the single steps are described in more detail in chapter 4.2.3.

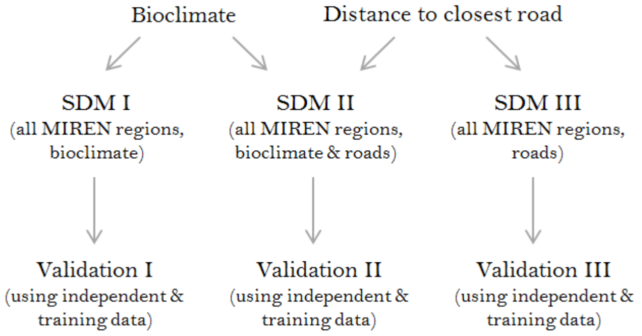


Figure 4: Workflow diagram of including roads in the SDM.

4.2.2 Downscaling bioclimatic data

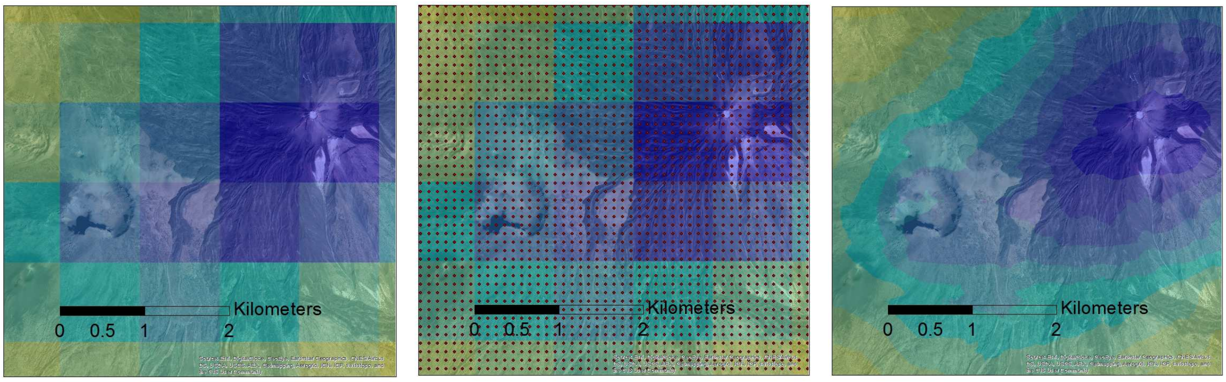
I downscaled the bioclimatic variables for **5 MIREN regions**: Northern Scandes, Canary Islands, Oregon Rocky Mountains, Australian Alps New South Wales and Australian Alps Victoria. I chose the regions based on their location, so that both island and continental systems in different hemispheres were represented. In each of the 5 regions, I downscaled each of the 8 bioclimatic variables (TAnnual, TWarm, TCold, PAnnual, PWarm, PCold, AI, PDD; see chapter 4.1.2) based on 6 topographic variables (Elevation, Slope, Northness, Eastness, Solar Radiation, Distance to Ocean; see chapter 4.1.3). It was not feasible to process all 11 MIREN regions within the timeframe of my thesis, because the downscaling calculations are very computationally intensive.

For each region to be downscaled, I created a **point shapefile** in ArcGIS with a grid size of 100 m. At the location of each point in this grid, I extracted the values of the 6 topographic raster files as well as the 8 bioclimatic raster files that I intended to downscale.

Based on this point shapefile, I ran an **Ordinary Least Squares Regression (OLS)** for each bioclimatic variable as response variable and the 6 above mentioned topographic variables as explanatory variables. The OLS serves as an intermediate step for the following more detailed Geographically Weighted Regression, which builds on the OLS-model. The OLS was computed in ArcGIS using the tool 'Exploratory regression'. If several variables were collinear (Variance Inflation Factor >7.5, shown in the output table of the OLS results), I selected only one of them to avoid multicollinearity effects (ESRI ArcGIS 2012c). The tool then performed a stepwise backward model selection and in the end, I chose the model with the lowest corrected Akaike Information Criterion (AIC) as regional model (ESRI ArcGIS 2012c).

Based on the explanatory variables of this regional model, I performed a **Geographically Weighted Regression (GWR)** (Li *et al.* 2010; ESRI ArcGIS 2012a; Su *et al.* 2012; Wang *et al.* 2012). A GWR takes into account the effects of geographic heterogeneity (i.e. non-stationarity), meaning that explanatory variables can have different effects in different parts of the region, e.g. on a mountain compared to a valley. This is done by fitting a regression model for every point in the shapefile. These local models are based on values that lie within a specified bandwidth around each point. I performed the GWR in ArcGIS using the tool 'Geographically Weighted Regression' with a fixed kernel type and a bandwidth of 500 (defines the extent of the kernel). Usually, the bandwidth should be calibrated separately for each GWR, but since these calculations are very computing intense and therefore not feasible within the timeframe of my work, I used the same bandwidth for all GWRs. After applying the GWR, I compared the corrected AIC values of both the OLS and GWR results to assess the effect of moving from a regional model (OLS) to a local model (GWR) (ESRI ArcGIS 2012b).

Based on these predicted values of the GWR that were calculated for each point of the 100 m point grid, I performed an interpolation to estimate the values between these points, thereby creating a continuous raster file that represents the downscaled bioclimatic data, i.e. the topoclimate. For interpolating, I used the **Inverse Distance Weighted (IDW)** method and defined 50 m as spatial resolution for the output raster files. It was not feasible to work with a 50 m point grid from the beginning due to the increased calculation time. The entire process of downscaling the bioclimatic variables is exemplarily shown in Figure 5.



original bioclimatic data ——► point grid for OLS and GWR ——► IWR: downscaled bioclimatic data

Figure 5: Illustration of downscaling bioclimatic variables.

In order to assess the effect of downscaling the bioclimatic variables, I applied the same species distribution model to both the downscaled and original bioclimatic data (5 MIREN regions). I compared the AIC values as well as the areas under the curve (AUC) of the receiver operating characteristic (ROC) (see chapter 4.2.3). The AUC was tested against independent data (Australian dataset, see chapter 4.1.1) as well as the training data (MIREN data for the 5 downscaled regions, 3032 absence- and 388 presence-points for *T. repens*).

4.2.3 Species distribution models (SDMs) for *Trifolium repens*

Specifying niche and distribution

A species' ecological niche as well as the relation between niche and geographic distribution can be defined in many different ways (Pulliam 2000; Araújo & Guisan 2006; Soberón & Nakamura 2009). Generally, a species' niche represents the whole set of environmental conditions that allow a population to exist indefinitely (Hutchinson 1957). In this framework, the **fundamental niche (FN)** of a species is defined as the combination of abiotic factors, such as climate, in which the species can theoretically maintain a positive growth rate. The FN corresponds to the geographical space where these favorable conditions are present, i.e. this space can potentially be occupied by the species. However, the FN is only a simplification of the actual conditions needed for a species to survive in a given area. In fact, biotic interactions (e.g. competition, predation and facilitation) strongly influence the subset of the FN that a species can really occupy, which is called **realized niche (RN)**. Moreover, while favorable abiotic and biotic conditions govern the potential distribution of a species, its actual areas of presence are also influenced by range dynamics, e.g. individuals might occur in unfavorable conditions due to source-sink dynamics or time-delayed extinction, and they might not occur in favorable condition due to dispersal limitations (Pulliam 2000; Guisan & Thuiller 2005; Soberón & Nakamura 2009; Jiménez-Valverde *et al.* 2011; Schurr *et al.* 2012). Especially non-native species have mostly not yet reached their full potential distribution in invaded regions (Elith & Leathwick 2009; Jiménez-Valverde *et al.* 2011; Lockwood *et al.* 2013).

A species' niche can be estimated either by a mechanistic (i.e. direct measurement of responses of individuals to different variables) or correlative (i.e. relating spatial data of species occurrences with ecological variables) approach (Soberón & Peterson, A. Townsend 2005). This niche information can then be extrapolated into geographic space to model the species' **spatial distribution** (Soberón & Nakamura 2009). SDMs can be created for descriptive (i.e. testing hypotheses) or predictive (i.e. temporal or spatial projections) purposes (Araújo & Guisan 2006; Elith & Leathwick 2009; Mouquet *et al.* 2015). In my case, I used a correlative approach and aimed at testing for the effect of roads on invasion probability as well as at predicting the potential areas of invasion by *T. repens.* Since I combined environmental factors (i.e. bioclimate) with a spatially explicit factor (i.e. distance to roads), the outcome can be described as the 'potential geographic distribution' of *T. repens* (Araújo & Guisan 2006).

Modelling method

As recommended when modelling the niche of invasive species (Jiménez-Valverde *et al.* 2011; Capinha *et al.* 2012; Petitpierre 2013), I used (1) distributional information from native and non-native regions (see chapter 4.1.1), (2) explanatory variables that are linked to the physiological requirements and limits of *T. repens* (see chapter 4.1.2) and (3) modelling procedures that avoid overfitting to the training data. SDMs can be modelled with different techniques, e.g. using geometrical, machine learning or statistical algorithms (Jiménez-Valverde *et al.* 2011). I used a regression model under R, version 3.2.5 (R Core Team 2016). Since the response variable of this model is recorded as presence-absence-data, i.e. binary data, and the model contains random effects, I applied a Generalized Linear Mixed Model (**GLMM**) to analyze the data (family: binomial). The random effects of the transects are nested within roads, which are nested themselves within regions, and the different years of the two surveys are added as additional random effect in a crossed order, i.e. (1|region/road/transect)+(1|year). The models were fitted with the function 'glmer' from the package 'lme4' (Bates *et al.* 2015).

Explanatory variables and model selection

I first computed a model based on bioclimatic explanatory **variables** only (SDM I): TAnnual, TWarm, TCold, PAnnual, PWarm, PCold, AI and PDD. In a second model (SDM II), I added distance to the closest road (DistRoad) in addition to the bioclimatic variables, as described in chapter 4.1.2. A third model (SDM III) was based on distance to the closest road as the only explanatory variable. Since the variables of these three models are on very different scales, I **scaled** all variables by subtracting their mean and dividing them by their standard deviation, using the function 'scale' in R. This brings the values to a mean of 0 and the standard deviation close to 1. Additionally, DistRoad was log scaled to account for the rapid decrease of *T. repens* within the first meters away from the road and the much lower decrease further away from it (see Figure 8). Then, I visually explored if the bioclimatic variables were **collinear** (see Appendix III: Collinearity between bioclimatic variables) and if so, I selected the variables that are most proximal to the ecology of *T. repens* (Petitpierre 2013). Removing collinear variables is recommended, as it simplifies the analysis and helps to avoid overfitting (Guisan & Thuiller 2005; Jiménez-Valverde *et al.* 2011; Petitpierre 2013). The bioclimatic variables entering the full models were TWarm, TCold, PWarm, PCold, AI and PDD. **Interactions** between DistRoad and the bioclimatic variables were also tested. In both bioclimatic-based SDMs, I added **quadratic** terms for each of the bioclimatic variables. Since the MIREN regions are located in a wide variety of climate zones, *T. repens* could have range limits at both ends of the climatic gradients and therefore the relationships might not be linear (Seipel *et al.* 2012; Lembrechts *et al.* 2016). Based on these full models, I manually deleted one by one the variables with the highest p-value in order to find the model with the best fit, based on the lowest AIC value (Elith & Leathwick 2009).

Model evaluation

Based on the final SDMs, I created **prediction maps** for the MIREN region Australian Alps Victoria (30721 km^2). This was done in R, using the package 'raster' (Hijmans 2015). I first scaled the explanatory variables' raster files with the same values that were used in the SDMs, in order to make the coefficients of the SDMs and the raster files comparable. Then I applied the SDMs to these raster files using the function 'predict', which resulted in a map for each SDM that showed the probability (values between 0 and 1) of *T. repens'* presence, see Appendix V: Prediction maps SDM I, II and III. These predictions could then be tested against real presence-absence data of an independent dataset (see chapter 4.1.1). For testing the predictive performance of SDMs, it is recommended to use **independent data** (i.e. validation) instead of resampling the original dataset (i.e. verification) (Guisan & Zimmermann 2000; Araújo & Guisan 2006; Elith & Leathwick 2009; Newbold *et al.* 2010; Mouquet *et al.* 2015).

Model accuracy was measured in R with the area under the curve (**AUC**) of the receiver operating characteristic (ROC), using the function 'performance' from the package 'ROCR' (Sing et al. 2005). AUC is one of the most widely used accuracy measures in various disciplines, including ecology, and it shows the performance of a binary classifier, i.e. the ability of a model to discriminate between presences and absences (Liu *et al.* 2009; Newbold *et al.* 2010). The ROC plot shows the proportion of presence points correctly predicted as presence (i.e. true positive rate or sensitivity) against the proportion of absence points incorrectly predicted as presence (i.e. false positive rate or commission error) for all possible thresholds that can be used to divide presence from absence predictions (Newbold *et al.* 2010). These plots depict a curve and the area under this curve represents the accuracy rate (i.e. percentage of correct predictions). A value of 0.5 stands for the lowest predictive performance (equal to random guessing) and 1 means the highest predictive performance (predicting all presences and absences correctly) (Newbold *et al.* 2010). In addition to the AUC value, other measures can be taken into account for describing the predictive performance of SDMs (see Table 2). SDMs are generally susceptible to two types of errors: predicting suitable habitats as unsuitable (false negatives) and predicting unsuitable habitats as suitable (false positives) (Guisan *et al.* 2013).

It is recommended to report **sensitivity and specificity** separately (Lobo *et al.* 2008). Sensitivity is the true positive rate (fraction of all presences that have been correctly predicted as presences) and specificity the true absence rate (fraction of all absences correctly predicted as absences) (Lobo *et al.* 2008) and both measurements can range between 0 and 1. Especially regarding invasive species, this differentiation is important, since it is common to receive high commission errors (Guisan & Thuiller 2005). This can even be seen as desirable if one is trying to predict the potential distribution of an invasive species: to predict its occurrence where it does not occur yet, but might do so in the future

(Jiménez-Valverde *et al.* 2011). So instead of focusing on correctly predicting absences, one should emphasize the correct prediction of presences (i.e. sensitivity) (Jiménez-Valverde *et al.* 2011).

Table 2: Matrix of measures that describe the predictive performance of SDMs.

	Prediction	
Observation	present	absent
present	true presences (true positive rate = sensitivity)	omission error (false negative rate)
absent	commission error (false positive rate)	true absences (true negative rate = specificity)

I furthermore validated the SDMs with different **temporal and spatial subsets** of the independent dataset. First, I divided the independent dataset into data that has been collected before and after 2006 (because the SDMs are based on data that has been collected since 2006), in order to see if the SDMs can predict better the distribution of *T. repens* of the same time period. Second, I split the independent data into three subsets depending on their distance from roads (up to 100 m, 500 m and 1000 m away from roads) to see if the SDMs yield in better predictions on a similar spatial scale (MIREN data has been collected up to 100 m away from roads).

In addition to validating the SDMs with **independent data** as described above (which gives information about how well the model is able to predict to new situations (transferability)), I tested the SDMs against the **training data** (indicates how well the model is fit in absolute values (how well it describes the training data)) and reported the **AIC** values (to show which model has the best fit relative to the others, penalizing for the amount of variables).

5 Results

5.1 Effect of downscaling bioclimatic data

Downscaling the bioclimatic variables improved both the model performance and predictive power of the species distribution model. The AIC value decreased from 1779.3 (original bioclimatic data) to 1744.4 (downscaled bioclimatic data). When testing the model predictions against independent data, the predictive power was overall low, but downscaling the bioclimate slightly improved it. The model based on downscaled bioclimatic data had more predictive power (AUC 0.60, mean sensitivity 0.58) than the model based on original bioclimatic data (AUC 0.53, mean sensitivity 0.43). Whereas when testing the model predictions against training data, the predictive power was overall high, but no effect of downscaling the bioclimate could be noted. The model based on downscaled bioclimatic data had almost the same predictive power (AUC 0.91, mean sensitivity 0.71) like the model based on original bioclimatic data (AUC 0.91, mean sensitivity 0.72). The ROC plots are shown in Figure 6 and prediction maps can be found in Appendix IV: Prediction maps original vs. downscaled bioclimatic data.

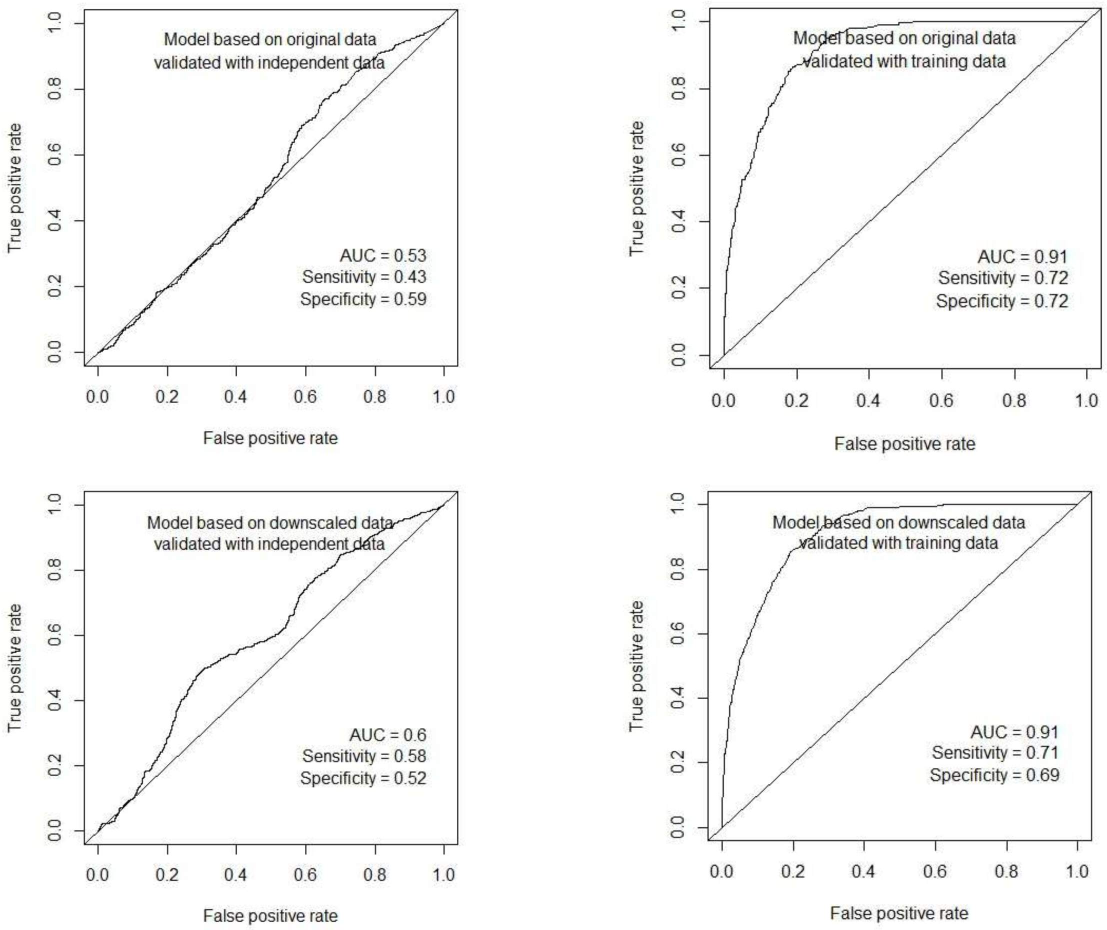


Figure 6: ROC plots showing the effect of downscaling the bioclimatic data.
Independent data (Australia): 626 presence and 5330 absence points for *T. repens*
Training data (5 MIREN regions): 388 presence and 3032 absence points for *T. repens*

5.2 Effect of including roads in the SDM

Including roads in the SDMs improved the model performance and especially the predictive power, being an even more accurate predictor than climate. The final explanatory variables in the first model SDM I were TCold, TCold^2, PCold, PCold^2, PDD and PDD^2. In the second model SDM II, the final bioclimatic variables were the same, plus DistRoad. Interactions between DistRoad and the bioclimatic variables proved to be not significant – perhaps it was not possible to detect them due to the different scales: DistRoad was measured over a distance of 100 m, which means that it spanned across only 1-3 bioclimatic raster tiles, which had a resolution of ca. 1 x 1 km (original data) respective 50 x 50 m (downscaled data). Comparing the AIC values for the three species distribution models, SDM II showed the lowest value (AIC 3059.4), followed by SDM III (AIC 3129.1) and SDM I (AIC 3399.7). When validating the models against the independent dataset, the predictive power was generally low with SDM III having the highest values (AUC 0.56, mean sensitivity 0.75), followed by SDM II (AUC 0.52, mean sensitivity 0.53) and SDM I (AUC 0.47, mean sensitivity 0.48). When validating the models against training data, the respective values increased a lot in general but did not differ much between the models. SDM II showed the highest values (AUC 0.97, mean sensitivity 0.92), followed by SDM III (AUC 0.97, mean sensitivity 0.85) and SDM I (AUC 0.95, mean sensitivity 0.83). The prediction maps are shown in Appendix V: Prediction maps SDM I, II and III and the ROC plots can be seen in Figure 7.

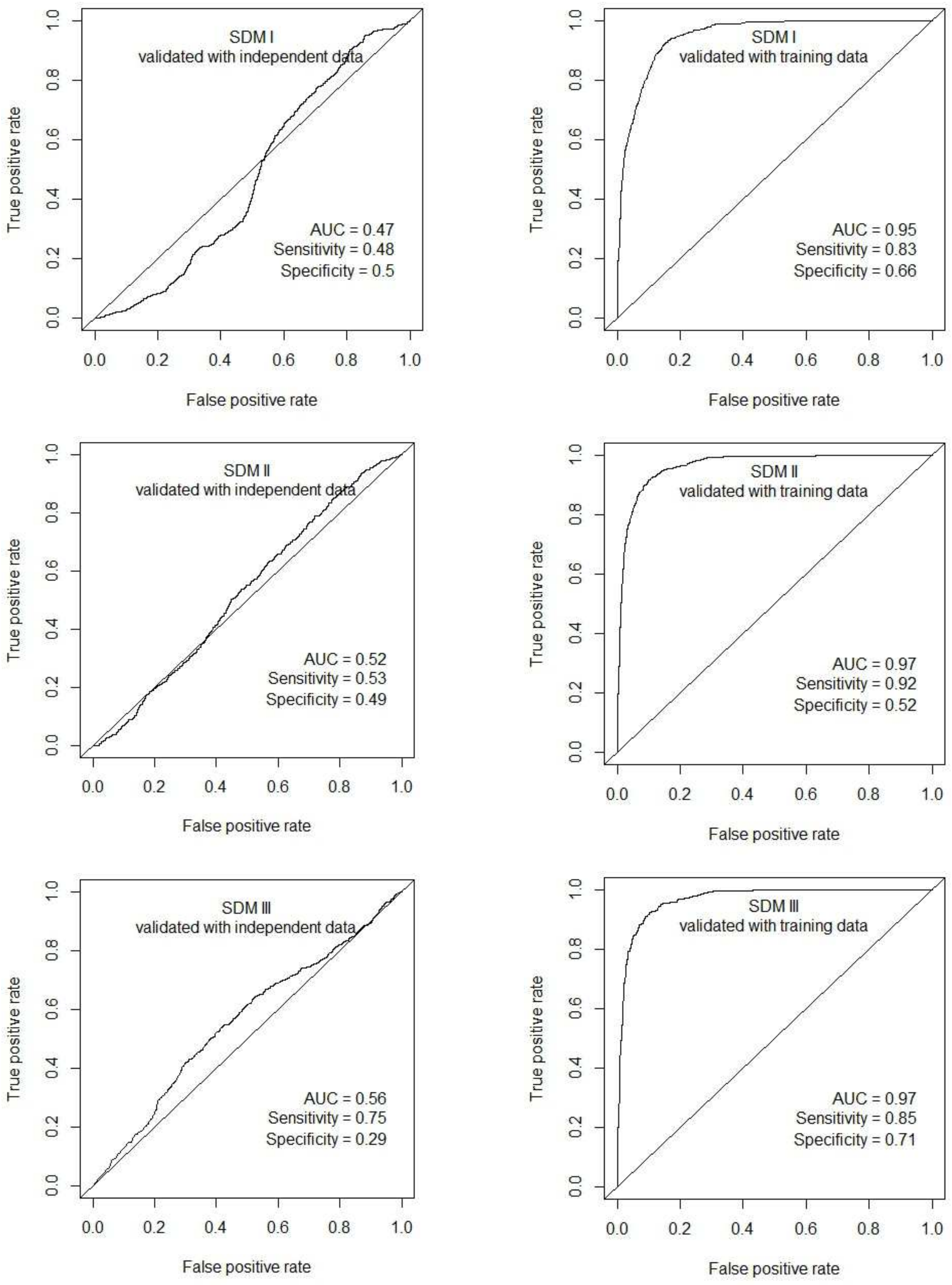


Figure 7: ROC plots showing the effect of including roads in the SDMs.
Independent data (Australia): 626 presence and 5330 absence points for *T. repens*
Training data (all MIREN regions): 757 presence and 6926 absence points for *T. repens*

Dividing the independent dataset into different time periods, it could be seen that all SDMs predicted the current distribution (since 2006) slightly better than the distribution before 2006. For SDM I the AUC value increased from 0.46 to 0.51 (mean sensitivity from 0.47 to 0.52), for SDM II from 0.51 to 0.55 (mean sensitivity from 0.52 to 0.56) and for SDM III from 0.55 to 0.58 (mean sensitivity decreased from 0.74 to 0.70). Dividing the independent data into different distances from the road and testing against SDM II and III (SDM I does not include roads), no clear pattern could be seen. SDM II predicted the distribution up to 500 m and 1000 m slightly better (both AUC 0.45, mean sensitivity 0.45 resp. 0.47) than the distribution within 100 m away from roads (AUC 0.44, mean sensitivity 0.48). SDM III on the other hand showed slightly higher predictive power for the areas up to 100 m and 500 m away from roads (both AUC 0.51, mean sensitivity 0.70 resp. 0.67) than for 1000 m distance (AUC 0.48, mean sensitivity 0.70).

6 Discussion

6.1 Interpretation of modeling results

6.1.1 Brief discussion of results

Modeling results provided evidence that downscaling bioclimatic variables to a finer resolution improved the prediction of *T. repens* presence. Therefore, **downscaling bioclimatic data** can be recommended for regions with heterogeneous topography, like the MIREN regions. Moreover, it can reduce common mismatches between the resolution at which species data is being collected and the one at which environmental predictor variables are available (Guisan & Thuiller 2005). The bioclimatic and topographic data used for the downscaling process is free of charge, but computing intensity and duration of the calculations (especially for calculating solar radiation and bandwidth for the GWR) might limit widespread implementation in practice. It is currently rarely applied (at least over large areas), but ongoing research seems promising, also with regard to investigating micro-refugia during climate change (Opedal *et al.* 2015; Meineri & Hylander 2016). As an alternative to the downscaling approach, which is already based on interpolated climatic data, actual field measurements would provide an even more accurate estimate of fine-scale climatic conditions, but also require much more effort (Opedal *et al.* 2015; Meineri & Hylander 2016).

When **comparing SDM I, II and III**, it could be seen that AUC and sensitivity values were constantly very low when tested against independent data. This could mean that the models are overfitted or incomplete, *T. repens* has not filled its potential niche yet in the validation area (Australia) or the independent Australian dataset is inadequate for validation. Efforts were made to avoid overfitting, but missing variables are likely (see below). Moreover, *T. repens* is probably not yet in equilibrium in its non-native range, so it can be assumed that is has not yet filled its potential niche. Especially considering the fact that the SDMs were based on roadside-data, where elevational range shifts become visible first (Lembrechts *et al.* 2016), it seems logical that the Australian dataset, which consists mainly of observations far away from roadsides, has not reached the same climatic conditions yet. Furthermore, the Australian dataset is atypical in several ways which might limit its validation quality (see below).

Including roads in the SDMs improved the model performance both when testing against training and independent data. For predicting independent data, SDM III showed even better results than SDM II. It indicates that for transferability to a new region, roads are even more accurate predictors than climate, maybe because climate is evenly favorable across the validation area or the climatic variables are not adequate here due to adapted *T. repens* varieties (see below). In regions with wide climatic ranges and for the upper range limit on a global scale, climate is still expected to be of great importance though (Alexander *et al.* 2009; Pollnac & Rew 2014).

Comparing **different timeframes**, all SDMs predicted better the independent data that was collected from 2006 onwards (during the same timeframe as the training data) than before 2006, which can be interpreted as an argument for considering residence time (see below). Sensitivity values of the two climate-based SDMs (SDM I and SDM II) were higher for the current data (since 2006) than the older data (before 2006) but for SDM III it was the other way around. This could indicate that in the validation area (Australia), *T. repens* has spread further away from roads and filled more of its climatic niche over time. It has to be noted though that the SDMs were fitted based on several MIREN regions in which the residence times of *T. repens* differ. Also, the discrepancy could be caused by sampling issues of the Australian dataset, e.g. different survey methods or sampling areas during the different timeframes, but no such patterns could be detected through the available information.

Assessing the predictive performance of the SDMs depending on **different distances to the road**, no remarkable discrepancies could be seen. The overall AUC values were very low (indicating no predictive power), but the sensitivity values for SDM III could be considered high enough (0.67-0.70) to draw conclusions. Since they did not differ much between the different distances to the road, it would suggest that the model is able to extrapolate on further distances than the scale of data collection (100 m).

6.1.2 Issues specific to my case

The extrapolation from small **scale** surveys to much larger areas can generally be problematic as it influences model robustness and realism (Elith & Leathwick 2009). Dispersal events of more than 100 m could not be detected by the survey method but can be expected to influence the species distribution on a regional level and over long time periods. Even though long-distance dispersal events usually happen only rarely, they play an outstanding role for the spread of invasive species (Lockwood *et al.* 2013). Long-distance dispersal in the direction of the roads is being captured by the SDMs (which is known to happen frequently) (Von Der Lippe & Kowarik 2007)), but not dispersal away from the roads into the natural vegetation. In this study, the extrapolation from 100 m to a regional level did not seem to reduce the predictive performance of the SDMs, as mentioned above. This assumption is also supported by the strong decline in *T. repens* occurrence with distance from road – in the MIREN surveys almost all *T. repens* individuals were found within 2 m next to the road, whereas at a 100 m distance from the road nearly no individuals were present (see Figure 8) – so it can be assumed that this clear trend also continues beyond 100 m away from the roads. It could furthermore indicate – if *T. repens* stays restricted to the very close proximity of roads – that a one-dimensional model, which considers only roads, would be sufficient. But this is not advisable because spread away from roadsides can be expected with time and satellite populations are ecologically important, even if they occur only rarely (Lockwood *et al.* 2013). The extrapolation of roadside data to entire regions is

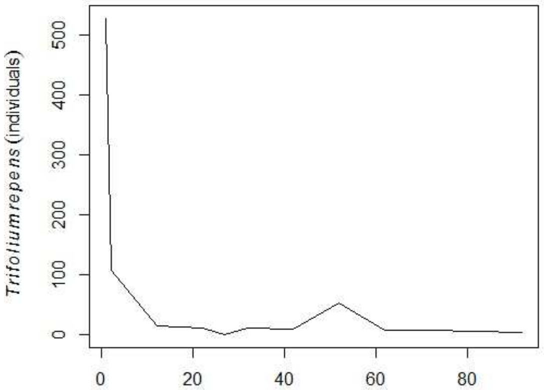


Figure 8: *Trifolium repens* decreases with distance to road.

supported by a study about building SDMs based on roadside samples, where Mccarthy *et al.* (2012) found that if the range of environmental gradients is represented in the roadside samples, they can be a valuable, unbiased data source for SDMs. Another issue in addition to the different scales is the mismatch between the **resolution** of the species survey and the bioclimatic predictors. The species data was collected only up to 100 m away from the road, whereas the bioclimatic variables had a resolution of circa 1 x 1 km (original data) respective 50 x 50 m (downscaled data). This means that several species points collected at different distances from the road are attributed with the same bioclimatic values, which is especially problematic for detecting interactions.

Another group of potential issues is directly related to **roads and roadsides**. In the independent dataset from Australia, it can be seen that *T. repens* is abundant along some of the roads, whereas it does not occur at all along others (see Appendix V: Prediction maps SDM I, II and III). These differences can be caused by the amount, type and origin of traffic (determining the propagule pressure), by the management and material of roadsides (see chapter 6.2) or just by random dispersal events. Thus, the SDMs could be improved by differentiating the road network into subcategories, characterized by traffic and roadsides. The high sensitivity value of SDM III confirmed a good predictive performance of the model and at the same time, a lot of false positives (low specificity value) indicated high potential for *T. repens* to spread more along roadsides – which suggests that theoretically, there are still plenty of roadsides left to invade in the Australian validation area. This result supports the above mentioned issue of missing propagule pressure along certain roads (many suitable roadsides with no *T. repens* yet). Furthermore, it should be considered that roads are not the only pathways for *T. repens* in mountains, but also e.g. hiking trails and cattle routes (Bear *et al.* 2006; Australian Government (Department of Health and Ageing) 2008; Leung *et al.* 2009; Müllerová *et al.* 2011; Ware *et al.* 2012). Even though roads can be seen as the major pathway, adding other types of pathways would probably improve the SDMs. Another issue regarding the roadsides is the fact that *T. repens* might occur there just because of constant propagule pressure and therefore represent sink-populations without the ability to reproduce. This would violate the assumption of the niche-concept where a positive growth rate is assumed and bias the predictions to areas further away from roads. Moreover, *T. repens* occurrence might be more correlated to small-scale microclimatic conditions in roadsides and other local conditions like soil properties (for *T. repens* especially soil moisture) and low competition through disturbance (Lembrechts *et al.* 2016) rather than larger-scale bioclimate, so the bioclimatic values derived from *T. repens* occurrences along roadsides might not be precisely representative. In this study, I cannot disentangle the effects of propagule pressure and favorable growing conditions on the success of *T. repens* along roadsides. Plant invasions along roadsides can be differentiated into vertical spread (higher in elevation) and horizontal spread (away from roadsides). The upper range limit (establishment of a species) in alpine environments is mainly determined by climate, whereas the lower realized range as well as the spread away from roadsides (growth after establishment) seems to be influenced mainly by native plant communities (Araújo & Guisan 2006; Alexander *et al.* 2009; Pollnac & Rew 2014; Lembrechts *et al.* 2016). Also Roux *et al.* (2012) found that species altitudinal ranges were more accurately predicted when including the cover of dominant species than when using abiotic variables alone. The effect of the present vegetation changes though, as facilitation gains importance over competition in higher elevations (Lembrechts *et al.* 2015).

Generally, **regional variations** of explanatory variables compared to a global model can be expected, e.g. certain climatic conditions may be biologically meaningful to a species in one region (actually restricting its geographical range) whereas other variables may have a weak or no impact (Rödder & Lötters 2009). This is especially true for *T. repens* as it has many genotypes and can adapt to a wide range of soil and environmental conditions (Lane *et al.* 2000). For example in the Australian validation area Victoria, grass competition and summer moisture stress are seen as the main environmental constraints limiting the performance of *T. repens* (Lane *et al.* 2000). But existing vegetation was not considered in my models and PWarm (precipitation of the warmest quarter), which could have served as a proxy for summer moisture stress, did not prove to be significant on a global level and was therefore not part of the models either.

In addition to such regular regional differences, the **Australian dataset** is atypical in several ways, which could explain the low predictive power of the SDMs in this region. First, *T. repens* has been introduced to Australia already in the late 18th century (Bear *et al.* 2006; Australian Government (Department of Health and Ageing) 2008) and this long residence time has allowed the species to adapt and spread. *T. repens* is considered a significant environmental weed in south eastern Australia, mostly because of its high adaptability – the current growing zone is estimated to be about 6 million ha with the potential to increase to at least 16 million ha (Australian Government (Department of Health and Ageing) 2008). It is found even in the alpine zone (but here, only on the verge of walking tracks) up to 2019 m and grows mostly in disturbed but also in natural areas (Bear *et al.* 2006; Pickering & Hill 2007). In the natural vegetation, *T. repens* is already so widespread that control is considered impracticable (McDougall *et al.* 2005). Especially along creeks and in mesic grasslands, it can form mats and outcompete native species (Godfree *et al.* 2006). Second, *T. repens* has been intentionally introduced in the Australian Alps on pastures as well as for soil stabilization on degraded grazing areas and ski resorts (since the 1950s) (McDougall *et al.* 2005; Australian Government (Department of Health and Ageing) 2008). Recolonization of these areas by native species has been slow and many places are still dominated by the introduced non-native species (McDougall *et al.* 2005). Moreover, *T. repens* has become common in natural vegetation throughout the Australian alps since then (McDougall *et al.* 2005). In other studies in the Snowy Mountains of Australia, adjacent to the validation area, *T. repens* was also found to be common in disturbed areas like road and trail verges, ski resorts and disturbed subalpine grasslands – occurrences in natural areas were mostly restricted to woodland and grassland sites at lower elevations (montane and subalpine) (Bear *et al.* 2006; Pickering & Hill 2007). Including information about (historical) land use in the SDMs is therefore expected to greatly improve the predictions, as it is also generally recommended on a regional level (Seipel *et al.* 2012). Third, breeding programs for *T. repens* in Australia resulted in special varieties that are better adapted to cold climates and especially to summer droughts (Lane *et al.* 2000; Australian Government (Department of Health and Ageing) 2008). These adapted varieties in particular could explain the mismatch with the global bioclimatic SDMs (SDM I and SDM II).

6.1.3 General issues when modeling invasive species

In addition to the above mentioned issues which are specific for this study, there are some general problems with modeling the distribution of species (especially invasive species). First, SDMs only represent a snapshot view and invasive species are expected to be not yet in **equilibrium** with their environment in the invaded regions (Guisan & Thuiller 2005; Elith & Leathwick 2009; Rödder *et al.* 2009; Soberón & Nakamura 2009; Jiménez-Valverde *et al.* 2011; Václavík & Meentemeyer 2012; Lockwood *et al.* 2013). Therefore, it would be important to consider factors related to range dynamics, e.g. residence time and dispersal rate (Wu *et al.* 2003; Soberón & Peterson, A. Townsend 2005; Araújo & Guisan 2006; Brooker *et al.* 2007; Haider *et al.* 2010; Pyšek *et al.* 2011; Schurr *et al.* 2012). Correlative SDMs do not account for such range dynamics though, therefore the estimated niche might be biased (Schurr *et al.* 2012). In my case, *T. repens* might be absent from suitable environments due to dispersal limits (e.g. in areas further away from roads and on the Canary Islands) and present in unsuitable environments due to source-sink dynamics (along roads). Václavík & Meentemeyer (2012) found that SDMs calibrated at early stages of the invasion process are less accurate and tend to underestimate the potential distribution, whereas SDMs calibrated close to equilibrium are more accurate. Regarding plant invasions in mountains, residence time is sometimes correlated with the elevational limits of non-native species, because time is needed for either dispersal or genetic adaptation (see next paragraph) (Becker *et al.* 2005; Haider *et al.* 2010; Alexander *et al.* 2011; Pyšek *et al.* 2011). Also regarding the horizontal spread away from roads, non-native species tend to colonize disturbed habitats in the early stages of the invasion process and then expand to natural areas as the invasion unfolds (González-Moreno *et al.* 2015). Since *T. repens* is most likely not in equilibrium yet within the MIREN regions (non-native ranges), its full potential distribution is probably underestimated in my studies and the SDMs can only reflect general patterns but have limited predictive power.

Second, it cannot be assumed that species keep their same niche in novel areas. Even though species niches usually evolve only slowly, this **niche conservatism** is doubtable when it comes to invasive species (Guisan & Zimmermann 2000; Araújo & Guisan 2006; Elith & Leathwick 2009; Rödder & Lötters 2009; González-Moreno *et al.* 2015). Novel abiotic and biotic conditions can change the realized niche, especially biotic interactions can either facilitate (for *T. repens* e.g. release from predators like grazing cattle) or reduce (for *T. repens* e.g. biotic resistance from native community like a shading shrub layer) invasions – moreover, also the fundamental niche of a species can shift in novel environments due to rapid evolution of species (Guisan & Thuiller 2005; Soberón & Nakamura 2009; Jiménez-Valverde *et al.* 2011; Pyšek *et al.* 2011; Boyd 2012; Lockwood *et al.* 2013; Tingley *et al.* 2014; González-Moreno *et al.* 2015). Especially species with high phenotypic plasticity, like *T. repens*, can adapt well to new environmental conditions (Haider *et al.* 2010; Seipel 2010; Jiménez-Valverde *et al.* 2011; González-Moreno *et al.* 2015). These uncertainties related to niche conservatism can result in both under- and overestimation of a species' potential distribution. Some general trends have been found though. Often, invasive species are more widespread in non-native ranges than in their native range due to the lack of predators (Lockwood *et al.* 2013). Moreover, Tingley *et al.* (2014) found that within the native range, mainly biotic interactions are limiting, whereas in the invasive range species can expand to their climatic limits in the absence of limiting biotic interactions. And climatic niche shifts seem to be rare among terrestrial plant invaders (Petitpierre *et al.* 2012). When modeling the potential distribution of invasive species, it is generally recommended to include both the native range (where species is expected to be at distributional equilibrium) as well as non-native range (where novel biotic and abiotic conditions are represented) in the SDMs (Bradley *et al.* 2010; Jiménez-Valverde *et al.* 2011; Capinha *et al.* 2012), which has been done in this study. But still, underestimation of a species' potential distribution when projected to novel areas remains a common problem (Guisan & Thuiller 2005; Jiménez-Valverde *et al.* 2011; Lockwood *et al.* 2013; González-Moreno *et al.* 2015). This might be especially true in my case, because I included true-absence information in the SDMs, which can misrepresent suitable areas (Jiménez-Valverde *et al.* 2011).

Third, **model evaluation** is another main challenge for invasive SDMs (Araújo & Guisan 2006; Elith & Leathwick 2009). Conceptual considerations include the trade-off between optimizing accuracy versus generality (Guisan & Zimmermann 2000) and SMDs that aim at predicting invasions should be evaluated with regards to generality, using independent data (Araújo & Guisan 2006). Since this data usually represents the realized distribution of a species though, it cannot accurately test the model predictions that aim at predicting the potential distribution (Araújo & Guisan 2006), penalizing SDMs which estimate the potential distribution and favoring the ones which estimate realized distributions (Jiménez-Valverde 2012). Commission errors will mostly not be erroneous in this context, as areas of overprediction are of interest when evaluating risk of species invasions (Araújo & Peterson 2012). Model evaluation should therefore focus more on well-predicted presences than on efficient prediction of absences (Jiménez-Valverde *et al.* 2011). Further criticism focuses on the AUC as a measurement for validation, which is commonly used for testing the predictive performance of SDMs (Guisan & Zimmermann 2000; Elith & Leathwick 2009; Liu *et al.* 2009). Since AUC values give information about the discrimination capacity of the SDM, the values are naturally lower for widespread species, even if the SDM is accurate – it only represents the generalist nature of the species distribution (Lobo *et al.* 2008). So the AUC value provides information about the generalist or restricted distribution of a species in the study area, but it does not provide information about the performance of the SDM (Lobo *et al.* 2008). Moreover, the AUC value assumes equal costs for commission and omission errors, it is spatially independent (we have no information about the spatial distribution of errors) and it is positively related to the spatial extent under consideration and the relative occurrence data (Lobo *et al.* 2008). The latter argument should not be a problem in my case, since the AUC values are compared for the same validation area and the same species data. It is furthermore recommended to rely on AUC values only if true absences are available (which is true in my case) and the objective is the estimation of the realized distribution (which is not true in my case) (Jiménez-Valverde 2012). So the AUC values have to be critically interpreted, but in combination with reporting the ROC plots as well as sensitivity and specificity values, it can still provide valuable information (Lobo *et al.* 2008; Jiménez-Valverde 2012).

6.2 Implications for roadside management

Prediction maps based on the SDMs of this study cannot be directly used for management decisions in Victoria (Australia) since their validation was not successful there. Maybe the SDMs would have higher predictive power in other regions, where the distribution of *T. repens* is less influenced by land use and breeding programs. Generally, the aim of my study was to show general global patterns, whereas for management purposes also regional characteristics should be taken into account. Still, my results underline the importance of roads and roadsides in the invasion process in mountains, therefore adequate roadside management is crucial. This seems feasible, as the number of roads in mountains is limited and roadsides are easily accessible for monitoring and management. Compared to the effort it would take to control invasive plants once they have spread in the natural vegetation, thorough and continuous roadside management is surely more efficient (McDougall *et al.* 2011).

Preventive measures

In order to prevent the introduction and establishment of invasive species in mountains, several aspects can be considered. Generally, it is recommended that mountain regions co-operate (e.g. share information about species that are invasive in some regions, but not yet in others) and focus on areas of high conservation value (Ansong & Pickering 2013; Pauchard *et al.* 2016). This should be coupled with prioritization schemes for targeting invasive species that are expected to have the greatest impact (e.g. preadapted to cold climate), are likely be transported by vehicles (e.g. regarding size and morphology of seeds) and for which prevention or eradication is still possible (McDougall *et al.* 2005; Ansong & Pickering 2013; Pauchard *et al.* 2016). SDMs can add information on prioritizing species that are expected to invade high conservation value areas and others that are likely to stay restricted to roadsides. Local managers will also have to decide how to deal with ‘native invaders’, i.e. native species that expand their range due to climate change (McDougall *et al.* 2011) and along roads (Lembrechts *et al.* 2016).

When building a **new road**, the invasion risk should be taken into account, e.g. SDMs can help to find potential invasion-'hotspots' which should be spared of roads. For the actual building process, the use of adequate road and roadside material is crucial, e.g. the use of alkaline gravel in granite mountains can change the soil pH and consequently influence native plant communities (Müllerová *et al.* 2011). How far away from roads this effect can reach depends strongly on the slope of the roadside (Müllerová *et al.* 2011). During the building process, machines should be cleaned from seeds before entering the mountain area (McDougall *et al.* 2011; Ansong & Pickering 2013). For example the Department of Sustainability and the Environment in Victoria (Australia) offers machinery inspection and clearing workshops for their employees and contractors in order to reduce the spread of non-native seeds (Pickering & Mount 2010). Along road construction sites, disturbance to the natural vegetation should generally be minimized (Godfree *et al.* 2006; Pollnac & Rew 2014). Even though disturbance does not necessarily favor the establishment of non-native plants in alpine environments due to the higher importance of facilitation (Lembrechts *et al.* 2015), *T. repens* has been found to establish in mountains primarily at disturbed places, such as roadsides or freshly excavated areas (Godfree *et al.* 2006) since it has only moderate ability to compete with other weeds during early establishment (Food and Agriculture Organization of the United Nations (FAO) 2016). After road construction, when stabilizing the roadsides against erosion through sowing or planting, it is crucial to use only native plants (Von Der Lippe & Kowarik 2007).

But not only building new roads, also reconstructing **existing roads** can increase the risk of plant invasions (Gelbard & Belnap 2003) and the above mentioned measures can be recommended. Once the roads are in use, connectivity to other regions should be taken into account for risk assessment (Von Der Lippe & Kowarik 2007). Seed dispersal through vehicles depends strongly on the road material and weather conditions. Vehicles on unpaved roads and off-road tracks were found to collect more seeds than on paved roads, especially under wet conditions, due to mud sticking to the vehicles (Ansong & Pickering 2013). The distance over which seeds are transported is generally much longer under dry conditions (> 250 km) than under wet conditions (both on paved and unpaved roads) (Taylor *et al.* 2012). Rain can therefore on one hand increase the risk of seeds attaching to vehicles, but on the other hand also wash off seeds from cars and prevent long-distance dispersal (Ansong & Pickering 2013). It can be generally recommended to clean vehicles, especially before and after driving off-road (Ansong & Pickering 2013) and before entering sensitive areas (Taylor *et al.* 2012). Strategically located washdown facilities can support implementation (Pickering & Mount 2010). Furthermore, it can be considered to restrict access to high conservation value areas under wet conditions and to establish regulations for cleaning and inspecting vehicles before entering certain regions or countries, like e.g. New Zealand and Australia have already done so (Taylor *et al.* 2012). Again, certain regions or species can be prioritized with the use of SDMs. Establishing early detection systems along roadsides, expanding prevention measures into the neighboring lowlands and informing road users about the issue are further measures than can be taken in order to prevent plant invasions (McDougall *et al.* 2011).

Controlling established populations

Once a non-native species has established along mountain roads, management should focus on controlling further spread. Since most mountain invaders have a broad climatic niche (Alexander *et al.* 2011), they generally have the potential to become invasive over a wide range. For the vertical spread **uphill along roadsides**, the precautionary measures mentioned above are also valid in order to minimize seed dispersal. Moreover, dispersal can be reduced by mowing the roadsides. It has been found that mowing roadsides generally tends to reduce plant species richness and favor non-native plants (Forman & Alexander 1998), but it strongly depends on the right timing. If the roadsides are mowed before the target plant is seeding, the amount of seeds transported by vehicles can be reduced, so further spread can be minimized (Ansong & Pickering 2013). But for example for *T. repens* this is hard to achieve since it is flowering and producing seeds over a long time period throughout spring and summer (apart from the fact that it is able to reproduce vegetatively) (Australian Government (Department of Health and Ageing) 2008). In such a case, mowing could have the opposite effect and even increase the spread of seeds along roadsides, which is why it is highly recommended to clean the machinery before entering mountain areas (Pickering & Mount 2010). If the machines are cleaned, it could be worthwhile to mow in downhill direction (in order not to transport seeds uphill), but in case cleaning the machinery is not feasible, it is probably better to mow uphill in order to slowly reduce the seed load towards less infested areas. Other than mowing, also pollutants from exhausts and deicing salt from road runoff can affect non-native species richness along roadsides (Müllerová *et al.* 2011). For example *T. repens* is sensitive to salinity and its nitrogen fixation ability gets reduced (Lane *et al.* 2000).

After establishing along roadsides, non-native species can spread **away from roadsides into natural vegetation**, which is mainly influenced by properties of the vegetative community (Pollnac & Rew 2014; González-Moreno *et al.* 2015; Lembrechts *et al.* 2015). The potential speed and area of spread could be estimated using mechanistic distribution models. Biotic factors can either facilitate or hinder plant invasions (Pollnac & Rew 2014), with facilitation generally outweighing competition in higher elevations (Lembrechts *et al.* 2015). Due to this elevational difference, disturbance to the existing vegetation should be minimized at low and mid elevations in order to limit the spread of non-native species (Pollnac & Rew 2014). This is especially true for *T. repens*, which colonizes bare soil and is not very shade tolerant (Lane *et al.* 2000; Australian Government (Department of Health and Ageing) 2008). It has to be noted though that *T. repens* increases its ability to compete with other weeds with residence time (Food and Agriculture Organization of the United Nations (FAO) 2016). Besides avoiding disturbance, the transport vectors into natural vegetation should be controlled – e.g. cars going off-road, tourists walking into natural areas or horseback riding (Pickering & Mount 2010). It would be important to inform visitors about the issue and to promote the economic importance and public acceptance of preventing further spread (Pickering & Mount 2010; McDougall *et al.* 2011). Detection of non-native species that have spread into the natural vegetation is especially hard in mountains due to the rugged and remote terrain (McDougall *et al.* 2011). Yet, early detection is crucial, because it is more effective to control satellite populations instead of the edges of the main population when trying to reduce the spread of non-native species (Lockwood *et al.* 2013). One approach could be to offer a monetary reward for citizens who detect new infestations, as it is being done in the Rocky Mountains (USA) (McDougall *et al.* 2011). Once a non-native species has been detected away from roadsides, different measures can be taken – in the case of *T. repens* for example punctual use of herbicides or hand pulling when working in native ecosystems and applying nitrogen fertilizer (reduced competitiveness in soils where nitrogen-fixing gives it no advantage) and heavy grazing or close mowing (both reduce competitiveness to grasses) in anthropogenic areas (MacRae *et al.* 2005; Australian Government (Department of Health and Ageing) 2008). In the Australian Alps however, *T. repens* is considered impracticable to control due to its large seedbank, capability to spread vegetatively and because it is already too widespread in the natural vegetation (McDougall *et al.* 2005; Pickering & Hill 2007; Australian Government (Department of Health and Ageing) 2008).

7 Conclusions

Downscaling the resolution of bioclimatic variables and including roads in the SDMs both helped to improve **predicting** the distribution of *T. repens* in its non-native range. When modeling non-native species in mountains, both aspects can thus be recommended. The downscaling approach I used however requires much computing power and time, which might limit its implementation on a large scale in practice. Generally, major limitations remain when applying these models to a certain region, e.g. for validation or management suggestions. This can be partly explained by general issues about modeling non-native species (e.g. assumptions about environmental equilibrium or niche conservatism) but also by regional peculiarities. Additional local factors have great influence on species' distribution and should be taken into account in order to receive reliable predictions within a certain region (e.g. native vegetation, soil moisture, additional pathways for introduction, current and historic land use and residence time).

Still, even though the predictions had only limited validation on a regional level, my results underlined the global importance of roads as major pathways for non-native plants into mountain areas, as roads were an even more robust predictor than climate for the distribution of *T. repens.* Non-native species disperse along roadsides and often stay restricted to them for a long time before spreading into the natural vegetation. On one hand, this makes it feasible to prevent and control invasions **in practice**, since roadsides cover relatively little area and are easily accessible for monitoring and management, on the other hand it also requires constant, targeted effort for roadside management. Preventive measures to avoid the introduction of seeds (e.g. washing vehicles) should be coupled with measures to control further spread after establishment (e.g. adequate mowing). Special focus should be given to high value conservation areas and non-native species with high invasion potential (e.g. species pre-adapted to alpine climate).

The risk of plant invasions is expected to increase in the **future**, mainly due to climate change and intensified land use. With warming climate, not only non-native species but also native species can expand their ranges to higher elevations and alter mountain communities, potentially outcompeting endemic alpine species. Intensified land use adds to this risk, e.g. ornamental plants escaping from gardens, increased hiking activities and the construction of more roads. Therefore, efforts should be made both on a conceptual level (refine predictions) and in practice (improve management).

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Appendix

Appendix I: Characteristics of the 11 MIREN regions

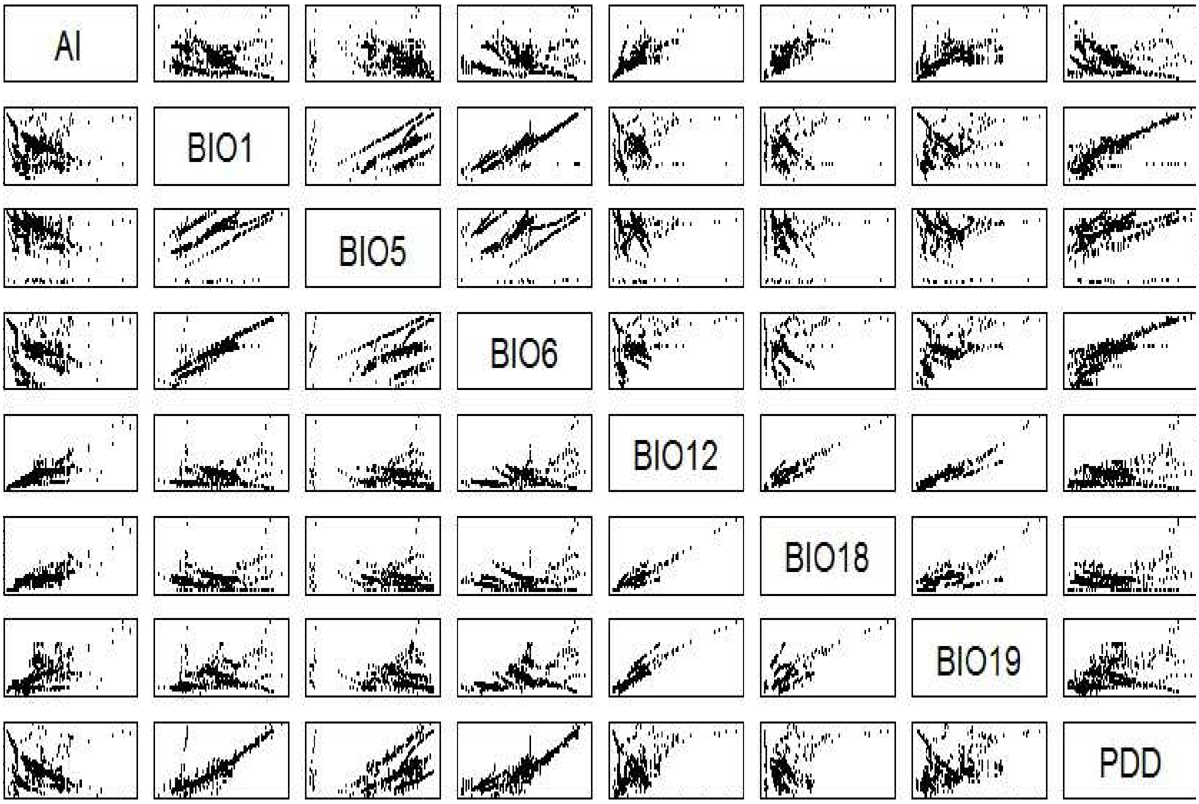
MIREN region	**Coordinates** (center of the region)	**Elevational range** (m above sea level)	**No. of roads**	**Max. distance from roads** (m)	**Years of the survey**	**Presence- and absence points for *T. repens***	**Presence-points for *T. repens***
Argentinian Andes	71°33' W 40°59' S	857 – 1678	3	100	2014	180	33
Australian Alps New South Wales	148°48' E 36°25' S	410 – 2125	3	100	2007 & 2012	1080	168
Australian Alps Victoria	146°54' E 37°16' S	205 – 1848	3	2	2012	60	37
Canary Islands	16°34' W 28°15' N	5 – 2250	3	100	2007	900	0
Central Chilean Andes	70°12' W 33°07' S	1895 – 3585	3	100	2007 & 2012	609	1
Hawaiian Islands	155°45' W 20°00' N	45 – 4192	6	2	2007 & 2012	476	122
Montana Rocky Mountains	110°24′ W 44°48′ N	1803 – 3307	3	100	2007 & 2012	1080	32
Northern Scandes	17°80′ E 68°19′ N	13 – 697	3	100	2012	300	22
Oregon Rocky Mountains	117°48′ W 45°18′ N	902 – 2265	3	100	2007 & 2012	1080	161
South Chilean Andes	71°24′ W 36°58′ S	274 – 1668	3	100	2007 & 2012	1068	86
Swiss Alps	7°12′ E 46°12′ N	411 – 1802	4	100	2007 & 2012	850	95
In total						**7683**	**757**

Appendix II: Explanatory variables used in other studies

Reference	**Explanatory variables** (**bold** = used in this work)	**Comments**
Broennimann *et al.* 2012	**Bio 1** annual max. temp. → **Bio 5** annual min. temp. → **Bio 6** **Bio 12** AET/PET → **AI** GDD above 5°C → **PDD** PET plant productivity index seasonality in precipitation → Bio 15	
Capinha *et al.* 2012	Bio 2 **Bio 5** **Bio 6** **Bio 12** Bio 14 number of rainy days per month	6 non-redundant climatic variables
Ficetola *et al.* 2007	**Bio 5** **Bio 6** **Bio 18** **Bio 19** human footprint (population density, infrastructure,…)	only those 4 Bioclim-variables were chosen to avoid collinearity
González-Moreno *et al.* 2015	**Bio 1** Bio 4 **Bio 6** Bio 9 Bio 15 **Bio 19**	tested all 19 Bioclim-variables, only those 6 were not collinear
Guisan & Theurillat 2000	**Bio 1** geology, rock cover, hydrology DEM • slope • aspect (northness & southness) • topographic position	some of these explanatory variables I used for downscaling the climate

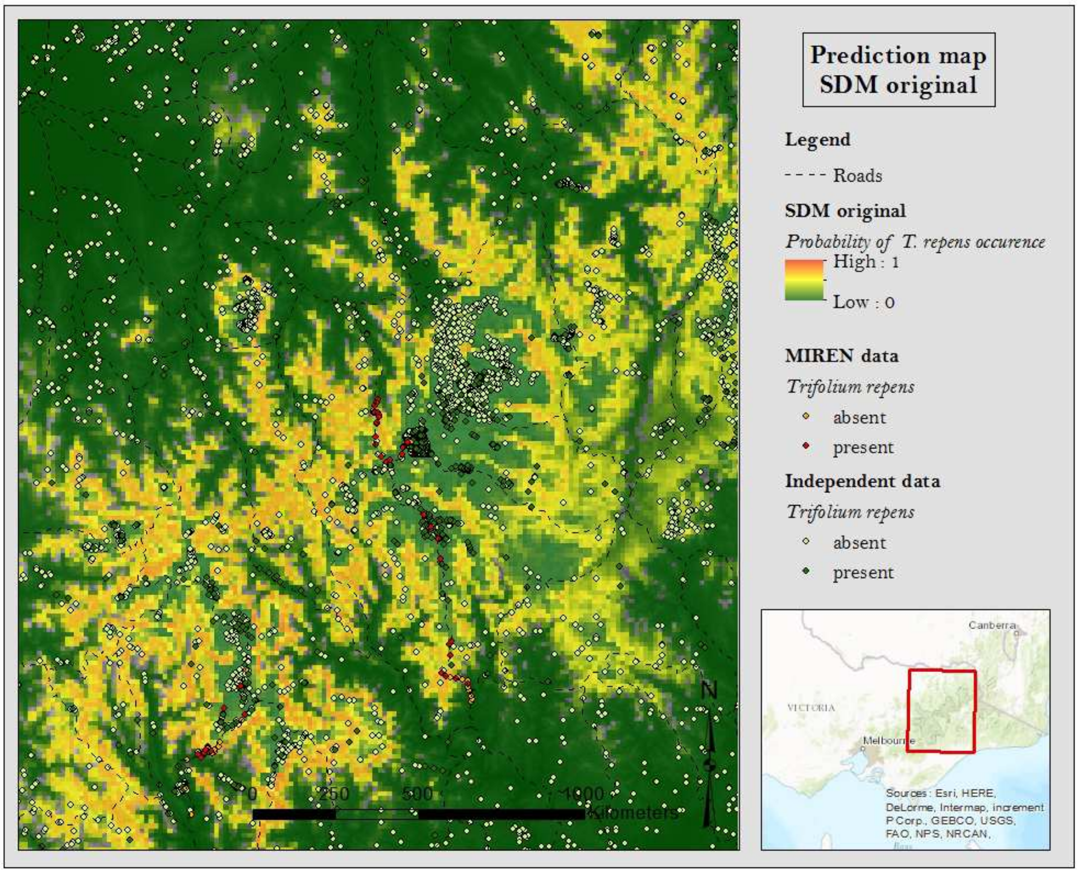
	• solar radiation black-and-white aerial photos infrared aerial photo (for soil moisture & snow cover)	
Petitpierre 2013	Precipitation seasonality → Bio 15 Mean moisture index of driest quarter Moisture index seasonality Mean temperature of warmest quarter → Bio 10 Mean moisture index of warmest quarter Precipitation of driest quarter → Bio 17 Mean moisture index of warmest week	8 most frequently included variables for different models of terrestrial plants (in ranked order)
Thuiller *et al.* 2005a	**Bio 1** **Bio 6** **Bio 12** **Bio 18** GDD → **PDD** AET/PET → **AI**	
Thuiller *et al.* 2005b	**Bio 6** GDD above 5°C → **PDD** AET/PET → **AI** plant productivity index	these variables affect plant physiology & growth
Tingley *et al.* 2014	**Bio 1** **Bio 5** **Bio 6** **Bio 18** mean humidity of the warmest quarter	variables were chosen because they are not correlated and influence the physiology of study species

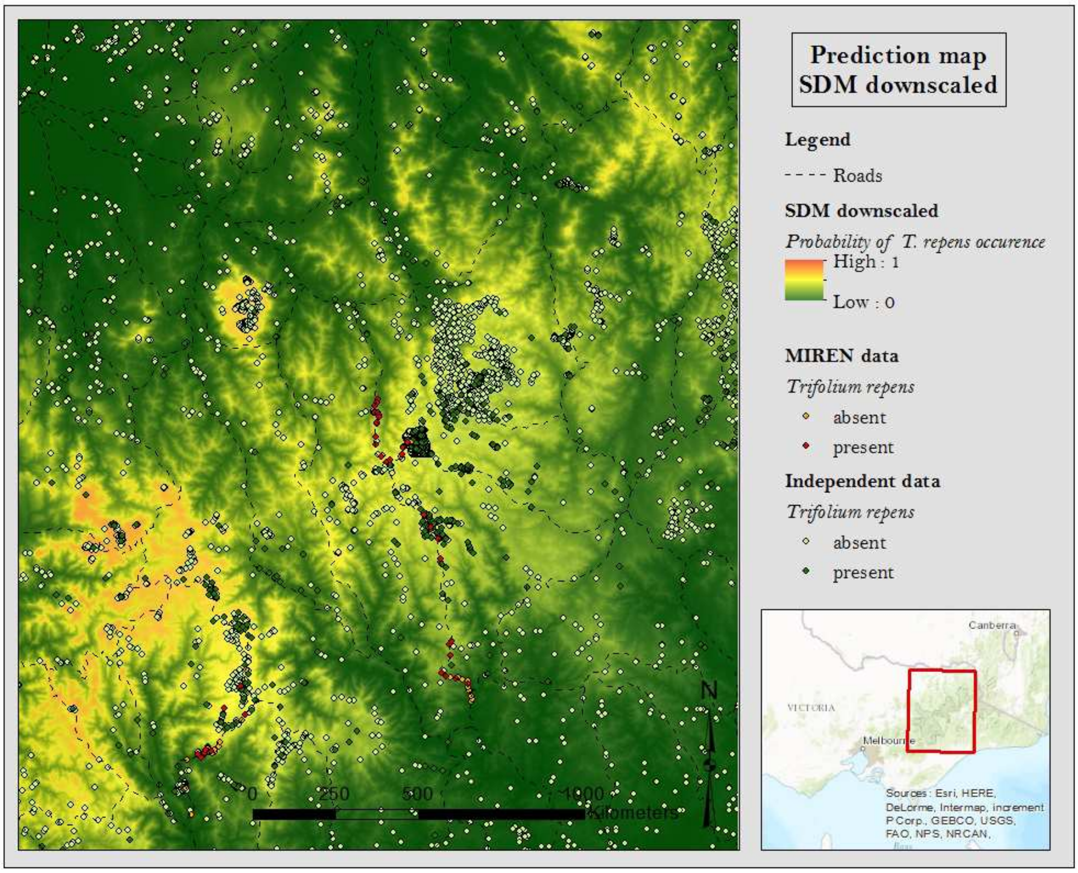
Appendix III: Collinearity between bioclimatic variables



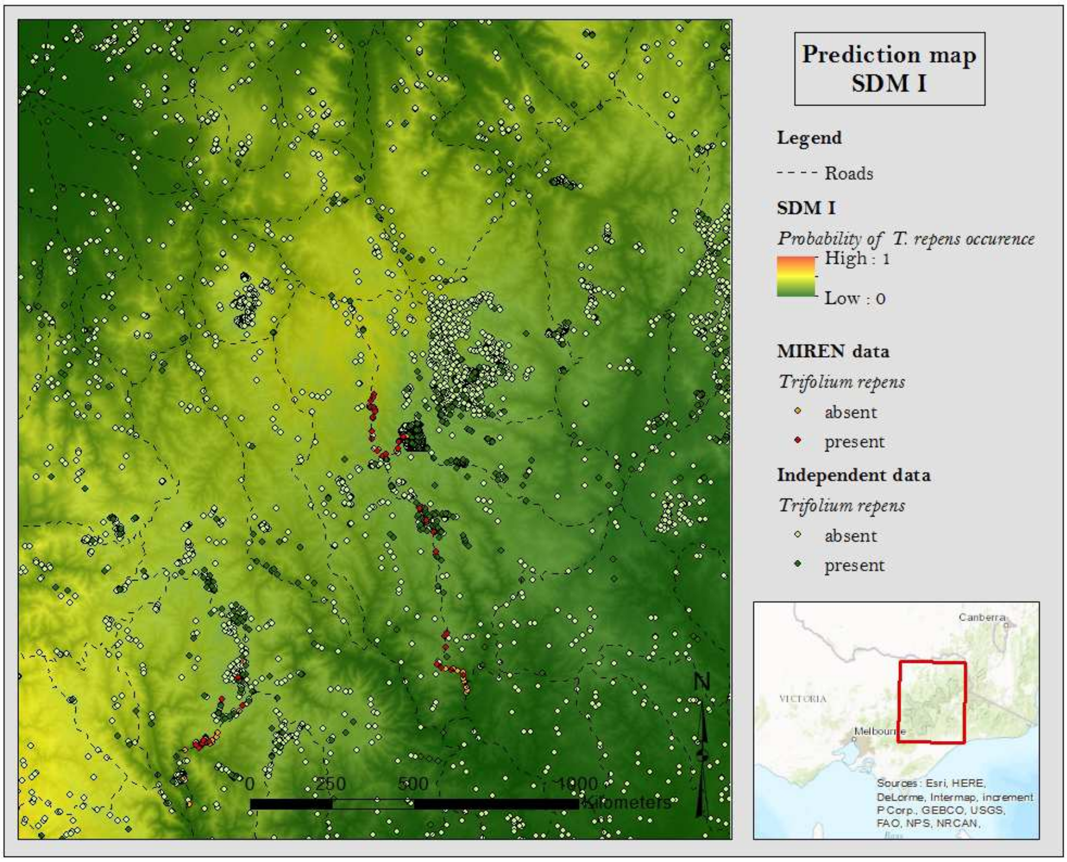
AI: Aridity Index
BIO1: Annual Mean Temperature (TAnnual)
BIO5: Max. Temperature of Warmest Month (TWarm)
BIO6: Min. Temperature of Coldest Month (TCold)
BIO12: Annual Precipitation (PAnnual)
BIO18: Precipitation of Warmest Quarter (PWarm)
BIO19: Precipitation of Coldest Quarter (PCold)
PDD: Positive Degree Days

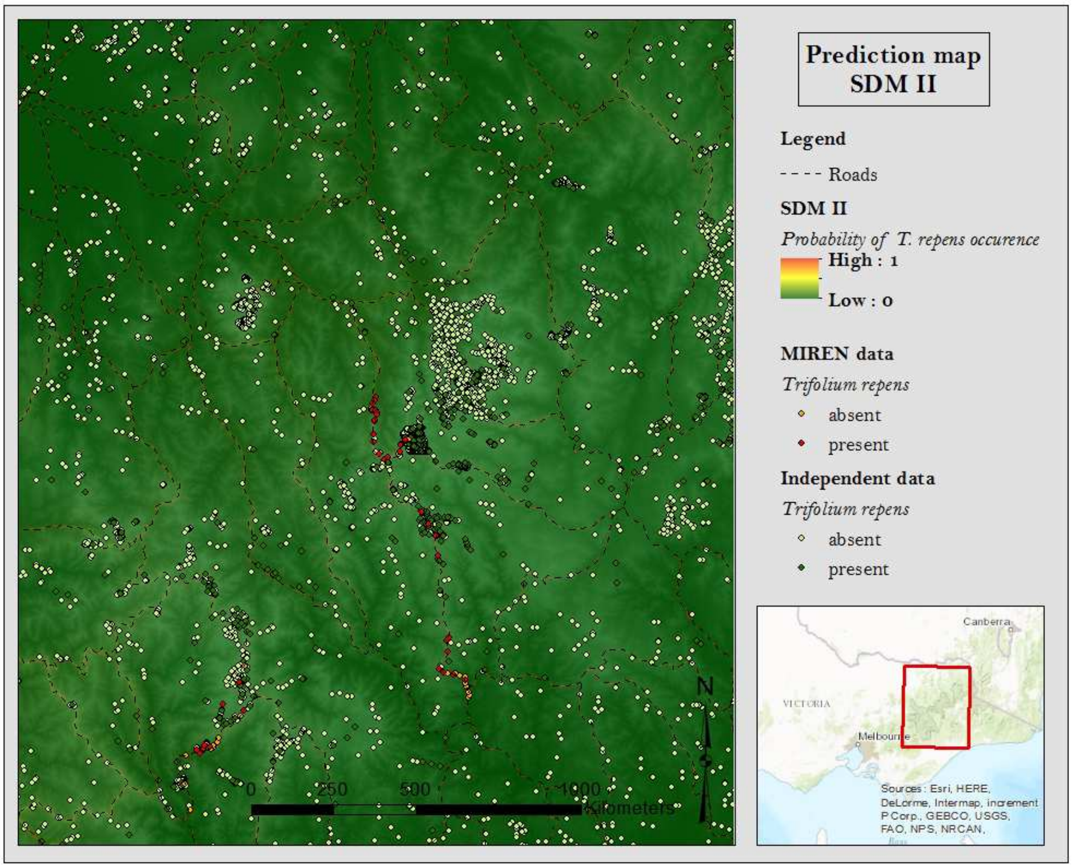
Appendix IV: Prediction maps original vs. downscaled bioclimatic data

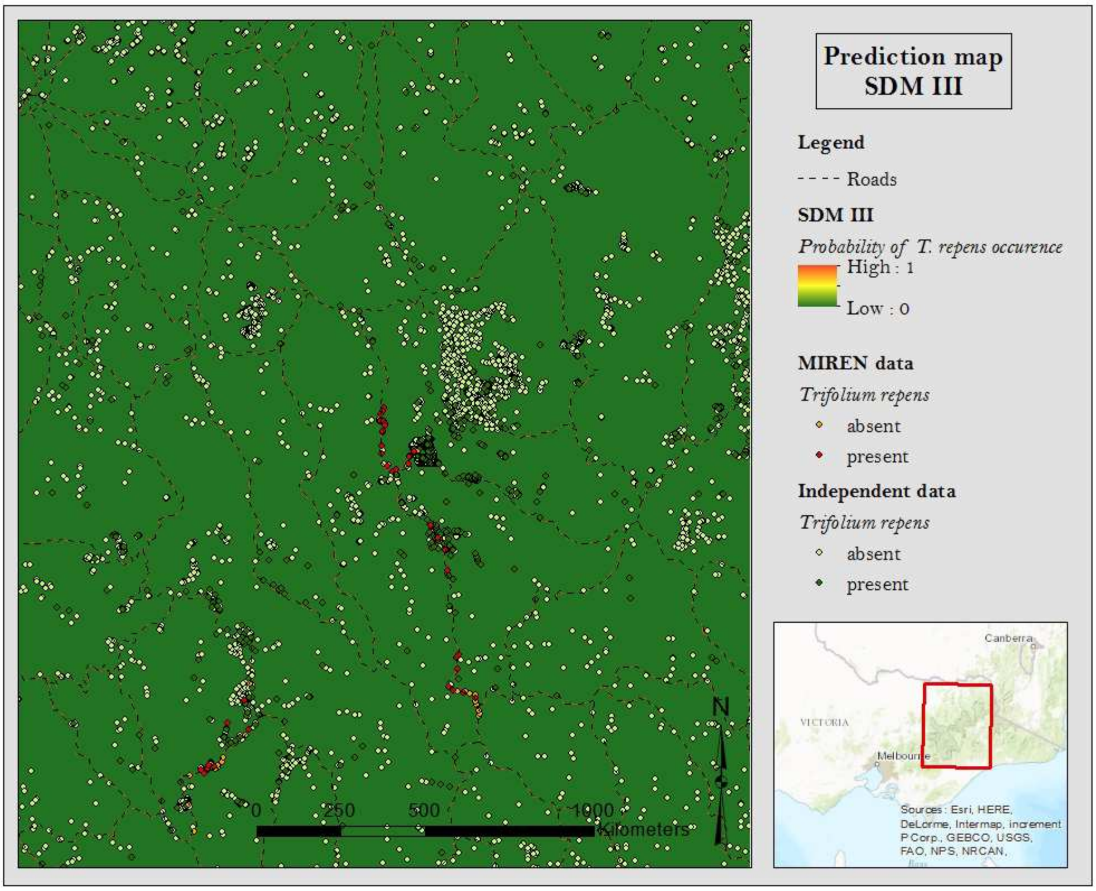




Appendix V: Prediction maps SDM I, II and III






Prediction map
SDM III
Legend
- - - - Roads
SDM III
Probability of T. repens occurence
High : 1
Low : 0
MIREN data
Trifolium repens
absent
present
Independent data
Trifolium repens
absent
present
0
250
500
1000
Kilometers
N
Canberra
VICTORIA
Melbourne
Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN,